TROPICAL RAINFORESTS

DIVERSITY AND CONSERVATION

Edited by
Frank Almeda
Catherine M. Pringle

PREMONTANE RAINFOREST
(Bosque pluvial premontano)

at 900 m on the Fila Costeña Ridge,
Pacific slope of the Cordillera de Talamanca.
(Photo courtesy of Frank Almeda).

TROPICAL RAINFORESTS: Diversity and Conservation

Edited by
Frank Almeda
and
Catherine M. Pringle

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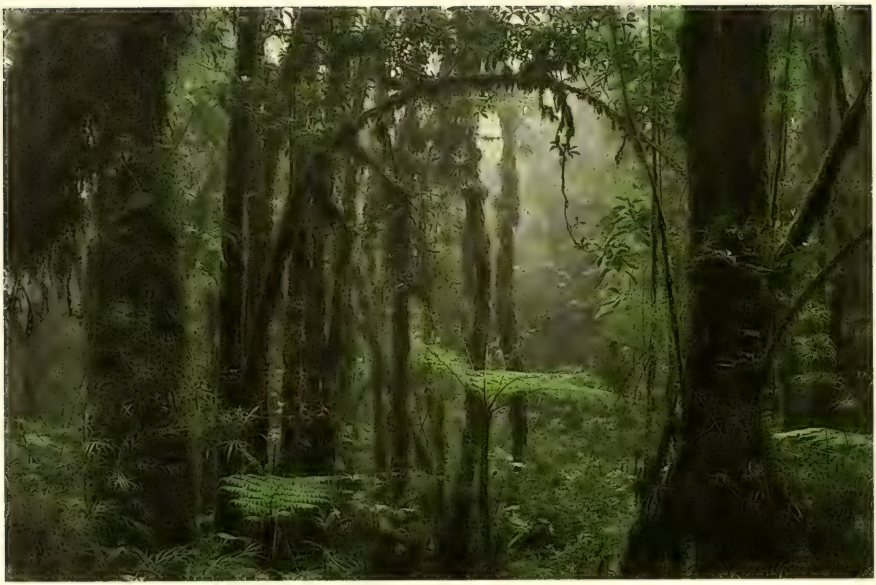
Dedicated to the government of Costa Rica
in recognition of its exemplary leadership role
in creating a national network of parks,
wildlife refuges, archeological sites,
and forest reserves.



MONTANE RAINFOREST

(Bosque pluvial montano)

at 2,900 m on the Caribbean slope of Volcan Barva, Parque Nacional Braulio Carrillo. This is one of four life zones and two transition zones included in the recently protected La Selva-Volcan Barva transect. (Photo courtesy of Gregory G. Dimijan).

PREFACE

This volume contains the papers presented at a symposium on "Diversity and Conservation of Tropical Rainforests," which took place at the California Academy of Sciences in San Francisco on 27 and 28 September 1985. The symposium was sponsored by the Academy and the Pacific Division of the American Association for the Advancement of Science.

Much has been written about the extraordinary richness, beauty, and diversity of tropical forests, the plight of vanishing species, and the unharnessed consumption of non-renewable resources. Some reports note that an area of tropical forest the size of the state of Delaware is destroyed worldwide each week, and an area of tropical forest nearly the size of England is destroyed each year. If this rate of destruction continues, we are told that most tropical forests will disappear by the year 2050, with the exception of certain areas in western Amazonia, the Zaire basin, and the few isolated refuges preserved as parks and reserves. One can hardly ignore reports in the popular press about the untapped reservoir of riches harbored by tropical forests. By continuing to fell tropical forests we are squandering untold sources of potential foods, medicines, germplasm stocks for improving our crops, and other natural products that could contribute to human welfare. Tropical forests are home to the world's richest and most diverse assemblage of plant and animal life. Because we still know so little about tropical organisms, ecological processes, and species interactions, the need to expand our knowledge of tropical ecosystems has never been more pressing.

In a two-day symposium, we could not hope to do justice to the many topics that need to be addressed on tropical diversity and conservation. In organizing the symposium, we were selective in highlighting one successful conservation effort in Costa Rica to acquire a land corridor linking La Selva Biological Station in the Caribbean lowlands with Parque Nacional Braulio Carrillo in the Cordillera Central. The entire 13,500-hectare corridor, which is now part of the extended park, represents the last tract of primary rainforest on Central America's Caribbean slope that spans an elevational gradient extending from sea level to almost 3000 m. This volume presents the conservation effort in the larger context of biological diversity and socio-economic development. It also provides historical documentation for a unique success story in international conservation involving the collaboration of conservation organizations, research institutions, the scientific community, philanthropic groups, and the private sector in Costa Rica and the United States.

An underlying concern throughout the planning process for the symposium was the desirability of assembling a roster of speakers and a selection of topics that would appeal to a broad spectrum of scientists, educators,

conservation organizations, government agencies, and the lay public. In addressing this audience our symposium speakers relayed their research findings and conservation perspectives in a series of essays as opposed to a strictly scientific format. The papers in this volume follow the symposium emphasis and reflect an intentional geographic bias toward the New World tropics.

Initial papers by Lovejoy, Myers, and Janzen address the broader issues of tropical forest diversity, the potential value of tropical species, and the effects of ecological isolation, deletions and additions on tropical ecosystems. Papers by Gliessman, Goulding, and Plotkin focus on some of the more applied aspects of tropical biology such as agroforestry, fisheries, and the important information to be gleaned from ethnobotanical studies. Mittermeier and Sterling highlight ongoing primate conservation efforts in Brazil and Madagascar. Gomez and Gamez and Ugalde introduce Costa Rica's internationally acclaimed park system and emphasize the link between conservation and socioeconomic development. Additional papers in this volume, all of which were presented on the second day of the symposium, focus on various aspects of education, research and conservation in Costa Rica. Stone recounts the history and development of the Organization for Tropical Studies (OTS) and its pivotal role in promoting graduate education and tropical research. Clark describes specific research, education, and ecodevelopment activities at OTS's La Selva Biological Station. Pringle documents the collaborative effort to protect the Braulio Carrillo Park extension, along with general findings of the first biological expedition into the area. Papers by Nadkarni, Stiles, Greene, and Hartshorn and Peralta present information on forest canopy dynamics, altitudinal migrations of birds, tropical predators, and forest types respectively. Much of the basic research presented by these authors was conducted at La Selva and Braulio Carrillo National Park. This crucial baseline information helps resource managers with their selection of protected areas and the implementation of long-term management policies. A summary essay by Raven draws attention to the world's poor and to the relentless pressure that poverty imposes on tropical forests. The immediate need to control such dangerous trends as overpopulation, energy depletion, and environmental abuse clearly suggests that the world is walking on a tightrope without a safety net.

We can speak proudly of our successes in preserving tracts of tropical forest, but these can only be considered temporary victories unless something can be done to relieve population/resource pressures. The problems in protecting wildlife and endangered habitats are manifold and the solutions are complex. Gliessman, in this volume, suggests that long-term protection of tropical parks and preserves can best be assured by land-use strategies that promote sustainable agricultural and forestry management systems on land that has already been cleared. Unfortunately the greatest onslaught of destruction is in

those developing nations that lack the financial and human resources to implement long-term protective measures. As Raven eloquently points out, tropical species are a part of everyone's heritage and we should all share the cost of their protection.

Many people and organizations contributed to the success of the symposium and subsequent preparation of this volume. Frank H. Talbot, California Academy of Sciences, gave his staunch and enthusiastic support to the project from its inception. Sandra Lelich, Deidre Kernan, and Kim Dodd assisted with organizational details and handled all local arrangements in San Francisco. The Servicio de Parques Nacionales de Costa Rica, the Fundación de Parques Nacionales de Costa Rica, the Organization for Tropical Studies, the International Nature Conservancy, and the World Wildlife Fund-US helped in a number of ways and responded expeditiously to our requests for advice and assistance. The California Academy of Sciences, the Pacific Division of the American Association for the Advancement of Science, and the World Wildlife Fund-US provided the generous funding, staff time, and materials that made production of this volume possible. Many others at the California Academy of Sciences assisted with various aspects of the volume. Mary Ford, Dustin Kahn, Barry Anderson, and Susan Middleton provided technical assistance with graphic materials and photography. Katherine Ulrich assisted with organizational and secretarial chores during the initial editing and reviewing phase. We owe a special debt of gratitude to the staff of the Pacific Division of AAAS for their untiring efforts on behalf of this volume. Alan E. Leviton reviewed all of the manuscripts and offered many helpful editorial suggestions. Margaret Berson did an outstanding job of copyediting the mansucripts and producing camera-ready copy for the printer. We and the authors are grateful to all these individuals and to the many anonymous reviewers who took time from their busy schedules to provide us with insightful comments that have helped to improve the entire volume.

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A CELEBRATION OF LIFE ON EARTH

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The tropical rainforest is where life reaches its fullest expression, where more forms of life are to be found than anywhere else on the globe, and where complex arrangements amongst species are encountered to an unparalleled degree. The ability of the life sciences to contribute to human welfare or, for that matter, the ability of biology as science to understand life on earth adequately, rests in large part on the knowledge waiting to be discovered in tropical forests. Our knowledge of these forests cannot be described as anything more than superficial; yet, at the same time, they are being obliterated at staggering rates. There is, as a consequence, a conservation imperative to protect the great diversity of tropical forest species and ecosystems in a very short time. But given the current ignorance, a conservation network cannot be simply established. Research on topics such as minimum size for reserves must go hand in hand with conservation action. A discussion of the research project on the minimum size problem in Central Amazonia will highlight the urgency of the Zona Protectora project in Costa Rica.

Life, even at the level of a single organism, is a remarkable phenomenon. The ability to make more of itself, and to build order and structure using energy usually derived from the sun, sets life apart from the inanimate majority of the universe. And what order and structure! If the DNA in a handful of soil, containing just bacteria, fungi, insects, and worms, can be equated to all the information in all 15 editions of the Encyclopedia Britannica combined (Wilson 1984), the information in a simple biological community is hard to grasp in its complexity. Extrapolating to the tropical rainforests, where for trees alone hundreds of species in a few hectares is commonplace, takes us to realms of complexity without parallel in the known universe. As the most complex systems in existence, the tropical rainforests deserve our

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attention and protection. Surely a key to understanding the universe, and to understanding life, of which we are a part, is our ability to study and understand the most complex manifestation known.

Almost everywhere in the world where tropical rainforests occur, they are in retreat, and in some places to the point of *extremis*. The plight of the Atlantic forests of Brazil, as exemplified by forest cover in the state of São Paulo, is one of the worst (Fig. 1). About 2% of the Atlantic forest remains, and in isolated fragments (a part of the story to which we will return later). Just the simple species/area rule-of-thumb that indicates a decrease in area by a factor of ten will reduce species numbers by a factor of two, will give the magnitude of the extinction problem there: roughly three-quarters of the multitude of species endemic to the region are in imminent peril of extinction.

Applying the same rule of thumb to the forests of Madagascar, of which 90% of the species (including the lemurs) are endemic, half the flora and fauna are in peril. These two examples, while extreme ones, are sufficiently echoed in other parts of the world to yield the realization that huge numbers of extinctions–hundreds of thousands of species–are in store during our lifetimes, unless drastic action is taken.

It is hard to belittle the problem both in terms of its importance for human welfare and in terms of the social, political, and economic forces that, of necessity, must be changed. It would be wrong to paint the picture totally in carbon black. It *is* possible to effect change, and the Atlantic forests of Brazil are a case in point. The gloomy projection for São Paulo in the year 2000 is no longer likely to occur. Protected areas have been accumulated one by one through action of both federal and state agencies, with assistance from World Wildlife Fund, and happily, in June 1985, Governor Montoro limited development along the entire remaining strip of the Serra do Mar by giving it special protected status. The governor of neighboring Paraná has since taken a similar action. But much remains in need of protection further to the north.

The plight of the Atlantic forests is not unique in the New World. As best as can be told, there were considerable Amerindian populations in the neotropical forests such that Santarém had a population capable of fielding 60,000 bows. The effect of the natural ecosystems was not inconsequential, and there is plenty of accumulating evidence of pre-Colombian vertebrate extinctions, especially on islands (Steadman 1985; Steadman and Olson 1985). Yet the effects are essentially minor compared to what is currently in train. The accounts of early navigators are often lyrical. For example, from the logs of Columbus regarding Hispaniola: "The Admiral said he never beheld so fair a thing–trees all along the river beautiful and green, and different from ours with flowers and fruits each according to their kind.

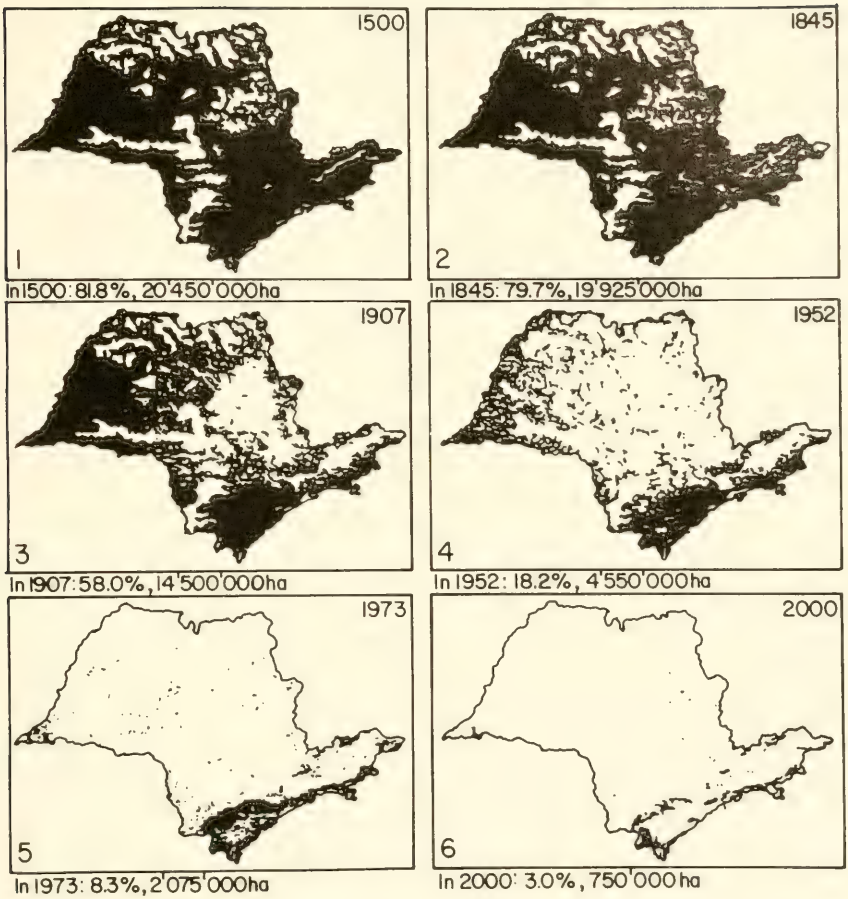

Fig. 1. Depletion of the forest area (black) in the state of São Paulo, Brazil, for the year 1500 to the projection for the year 2000. (From K. Oedekoven, 1980, Environmental Policy and Law 6:184-185).

Many birds and little birds which sing very sweetly." Today, of course, on the western end, Haiti is the most densely populated nation in the entire western hemisphere, deforested except in the most inaccessible places, with some of the lowest standards of living and highest infant mortality rates in the New World. It is hard to avoid the conclusion that the capacity of the land to support both tropical forests and people has been seriously overreached. El Salvador provides a similar, mainland version of the story.

Costa Rica is a very important part of the saga of neotropical forests

in part because of what it has been able to achieve in conservation, in part because of the problems that remain, and in part because of what has been achieved in both research and conservation at the almost legendary site of La Selva in the Caribbean lowlands. I am really an exception among tropical biologists of my generation in not having had initial training through the Organization for Tropical Studies, which perhaps allows me more freedom to state how incredibly important the programs conducted at La Selva have been. Certainly, this symposium would not have taken place without La Selva, for it was born of concern for La Selva's future. I cannot help but wonder whether the symposium would have in fact come to pass if it had had a different genesis, so great has been the influence on tropical biology of the OTS and its programs.

The importance of La Selva was already apparent to me when I first visited in 1971 as a newly minted Ph.D. The approach was still by boat at that time, but the increasing deforestation was hard to ignore. I subsequently became aware through conversations with John Terborgh of the great effects of fragmentation and isolation on natural communities, a topic of tremendous significance to efforts to protect the variety of life on earth. Obviously, this pertained to the situation of La Selva as well, and led to my involvement in efforts to protect it from isolation as early as 1977.

This concern also generated the 20-year research project in the Amazon, christened, perhaps a bit wishfully, the Minimum Critical Size of Ecosystems project. I would like to share some of the results to give an inkling of the magnitude and complexity of change the forests of La Selva would experience, were it to become isolated. The Minimum Size project was conceived as a program to generate data basic to the design and management of reserves, particularly in the Amazon. It also provides an experimental approach to the study of the theory of island biogeography, and most importantly to study the process of change induced by isolation of tracts of forest. It is a binational exercise conducted by World Wildlife Fund and Brazil's National Institute for Amazon Research (INPA) whose director, Herbert Schubart, is my co-investigator. Dr. R. O. Bierregaard, Jr. of World Wildlife Fund was for the first eight years the Field Director and conducts the ornithological portion of the study.

The basic research design is really very simple. It takes advantage of the Brazilian requirement that 50% of any Amazon development project remain in forest by turning the process of development into a giant experiment. Ranches north of Manaus are collaborating by arranging the geometry of their 50% to provide a size series of reserves ranging from 1 to 10,000 ha with replicates in all but the largest size class (Fig. 2). Reserves are demarcated and studied before isolation, providing baseline data from the forest in primeval state. The largest block of forest will change so slowly relative to those of

smaller size that the data from it can serve as another form of control, at least for the two decades of research planned at this point. The tiny reserves will provide preliminary insights into the changes induced by isolation, and each successively larger size class of reserves will provide more complex insights but more slowly. Recognizing that changes in larger reserves will still occur centuries hence, the Brazilian government is conferring protected status upon them so generations of future scientists can have access to them as ecological benchmarks. Indeed, the number of places on earth where a scientist can go and make measurements to compare with ones taken previously, or where scientific data can accumulate with respect to a particular site, is ridiculously small. La Selva, of course, is one of these.

Some of our first results involved the bird community of the understory, which was and is regularly sampled using mist nets. Species encounter functions (Fig. 3) were calculated from the banding data from the first 10-ha reserve isolated in May 1980, starting at various points subsequent to that isolation. The later the start of the data set, the more slowly the species encounter function rises, thus indicating an increasingly impoverished bird community. In the space of just a few months major reduction occurs in bird diversity (Bierregaard, Jr. in prep.; Lovejoy et al. 1983; Lovejoy et al. 1984).

Fig. 2. Aerial view of a 10-ha isolated reserve, part of the Minimum Critical Size of Ecosystems project. (Photo by R. O. Bierregaard, Jr.).

One would anticipate slower species loss and less final reduction in bird diversity with increasing area.

But the story is more complex. Capture rates doubled (Fig. 4) when the first two reserves (one 10-ha and one of a single ha) were isolated. Then they tapered off. Apparently the reserves were suffering an overcrowding problem superimposed on the area effect. With the next set of isolations in 1983, a similar elevation (Fig. 5) in capture rate was recorded with one interesting exception. This was a 10-ha isolate separated on three sides by only a 100-meter strip of clearing from a large block of forest. In this instance the large block probably absorbed the bulk of the refugees (Lovejoy et al. 1986).

The refugee birds might choose such a large block in preference because of the reduced intensity of interaction with resident birds. Certainly survival or persistence, as measured by rate of recapture, seems to be reduced in isolated as opposed to non-isolated areas (Bierregard, Jr. in prep.; Lovejoy et al. 1986) (Fig. 6). And the reserves in the early days after isolation are a bustle of bird activity and bird calls.

A further complication comes from looking at the influence of the very sharp edge on the bird community. Bird netting in the understory 10 and 50 meters in from the edge of a large block of forest yields reduced numbers of

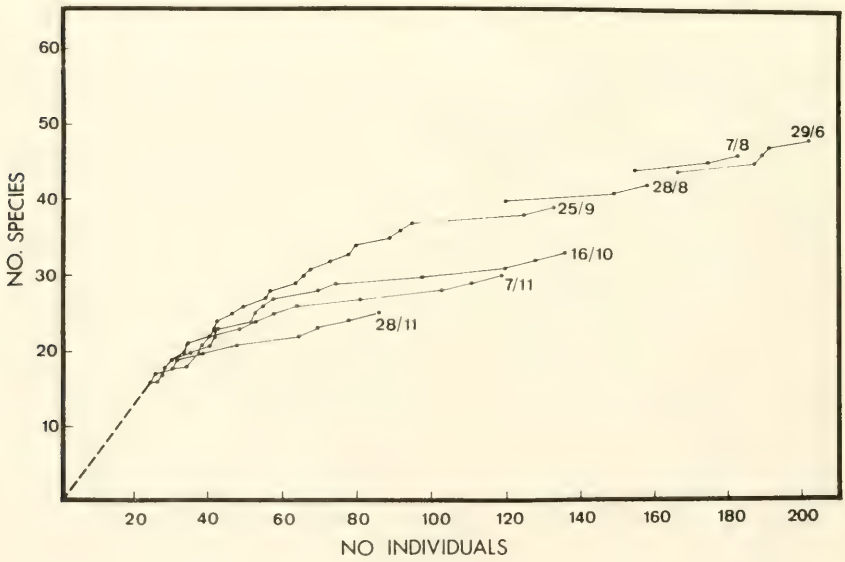

Fig. 3. Species encounter functions (number of species with increasing number of individuals sampled); dates (day/month) indicate initial date used to calculate a curve. The earliest curves are not plotted all the way to the origin for ease of interpretation. (From Lovejoy et al. 1984).

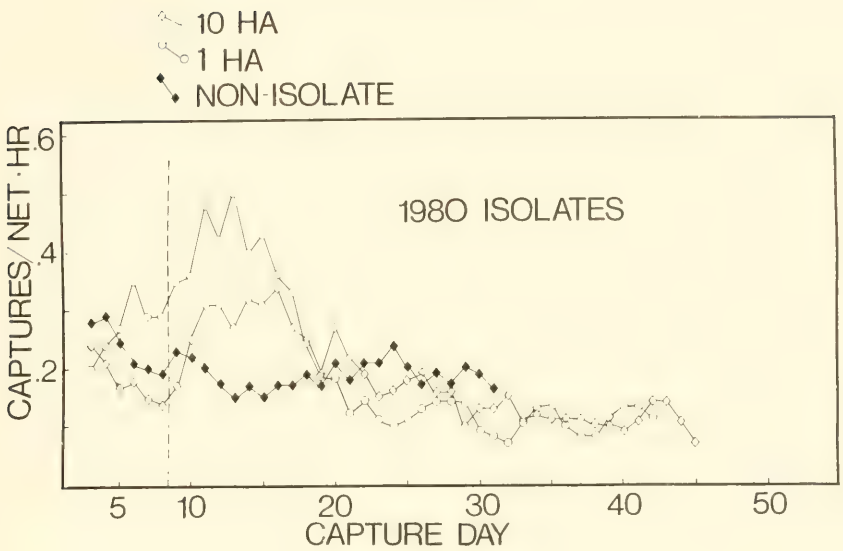

Fig. 4. Capture rates for understory bird community in 1980 isolates. Broken vertical line indicates point of isolation. (From Lovejoy et al. 1984).

individual birds (36%) at 50 meters and even more reduced numbers (60%) at 10 meters, as well as reduced numbers of bird species (47 and 28, respectively). The birds appear to be avoiding the edge and the increased light associated with it (Lovejoy et al. 1986).

This means that the reduction in bird diversity indicated by the species encounter function is a mélange of three factors: influence of edge, overcrowding, and area effects. To learn about area effects, attention must be switched from 10-ha plots to those of 100 ha.

Butterflies give a different picture of edge-related effects. Species numbers decline after isolation and burning of the felled trees, but rise subsequently to levels higher than at isolation. This is because the surrounding environment becomes highly favorable to light-loving species characteristic of forest openings and edges. Those then invade the forest interior, disrupting the existence of forest interior species as they compete for food resources and mating sites. Keith Brown (in prep.) estimates the extent of this edge effect as penetrating 200 to 300 meters into the forest, meaning only a central 25 to 30-ha core would have an intact forest butterfly community in a 100-ha reserve (Lovejoy et al. 1986).

The woody plant community shows changes much earlier than anticipated, probably in relation to strong microclimatic change deriving from surrounding pasture in place of forest. As much as 4.5°C difference in

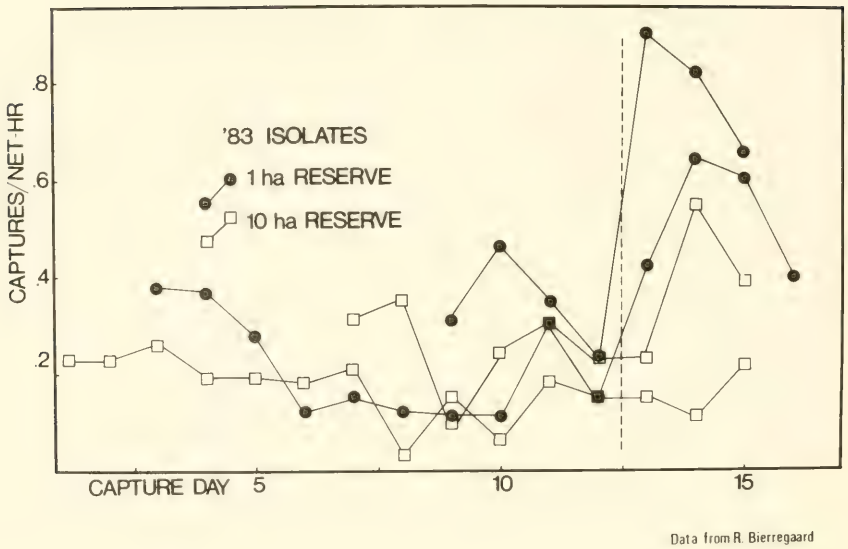

Fig. 5. Capture rates for understory bird community in 1983 isolates, showing the 10-ha isolate with no elevation in capture rate after isolation. Broken vertical line indicates point of isolation. (From Lovejoy et al. 1986).

temperature and 5-20% difference in relative humidity occurs between forest edge and 100 meters inside, with strong effects (in initial measurements) at 20 to 40 meters (Lovejoy et al. 1986). Doubled tree mortality rates, compared to normal, occur in isolated reserves, primarily because of increased numbers of standing dead trees. At the margin exposed to prevailing winds, tree falls increase dramatically. These dramatic changes in the physical structure of the forest must have strong effects on many other species.

Primates show differing response to isolation largely consistent with what might be expected from the size of their home ranges. The most interesting data involve the golden-handed tamarins, which have home ranges for troops on the order of 30 ha. In intact forest plots of 100 ha, these home ranges are quite distant from those of neighboring troops. In the one isolated 100-ha reserve, the three troops closely abut one another; it is not clear whether this closer-than-normal association can persist (Rylands and Keuroghlian 1985; Lovejoy et al. 1986).

Army ants normally occupy 30 ha per colony and their usefulness in flushing insect prey for ant-following birds is limited to that part of their three-week cycle when they are in swarming state. A single colony will not suffice to support the ant-following birds and, not surprisingly, neither ants nor birds survive in small one- and ten-ha reserves. But 100 ha and three

colonies might suffice. This appeared to be the case in the first 100-ha isolate, but the system failed to persist after the tiny tongue of forest connecting it with a larger block was cut.

The foregoing glimpses of the changes induced by isolation suggest the kinds of problems that would ensue were La Selva to be isolated. Its value for research on normal tropical rainforest biology as well as its value as a training ground for biologists would experience progressive erosion. Fortunately, the wedge of forest connecting it to the montane forest park of Braulio Carrillo was and is intact. That has provided a wonderful opportunity in itself for science and conservation—namely, the chance to protect an altitudinal gradient. We must be able to study gradients if we are to understand how the living world is structured. Species at the ends of gradients are tremendously important, for they tell us the limits under which life as we know it can exist, and how those species have solved the problems of living at such conditions.

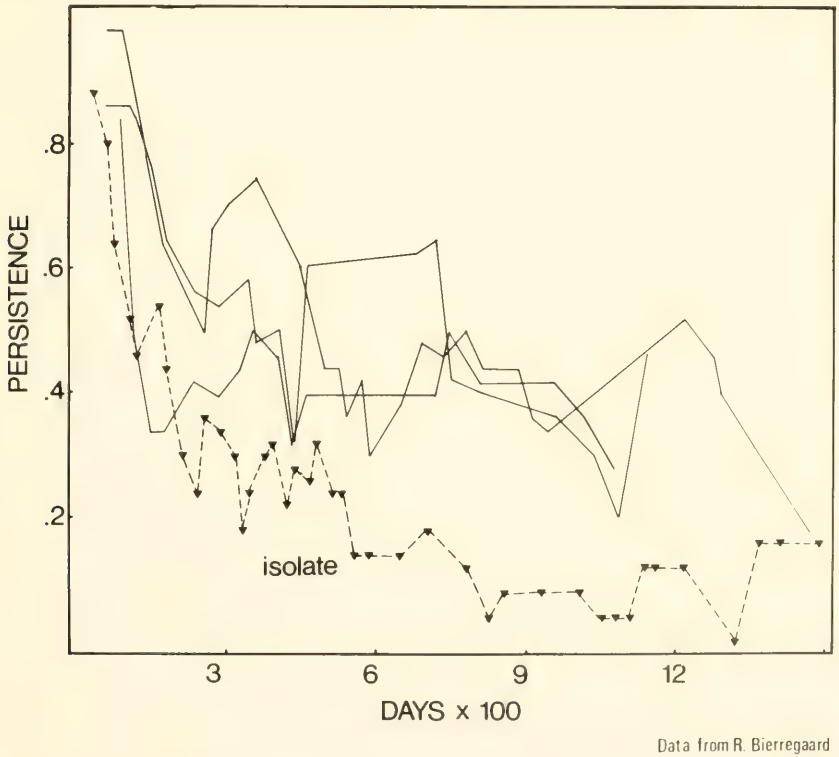

Fig. 6. Persistence as measured by running three-point averages of the percentage of each day's captures that were from the original cohort. Solid lines indicate non-isolated reserves. Data from R. Bierregard.

So, beyond the security the forest wedge provides La Selva against problems incurred by isolation, it is important to protect the gradient and ensure against its being cut along with linking species and processes.

Costa Rica's visionary former president, Daniel Oduber, had promised me that he would protect what is currently the Zona Protectora and which, after an unprecedented fundraising effort (by World Wildlife Fund, the Nature Conservancy, the Organization for Tropical Studies, and the Costa Rica Parks Foundation), Costa Rica has at long last converted to National Park status. However, Oduber ran out of time in office. Then the world energy crisis and the international debt problem struck, mirroring the ecological links between nations. Scientifically naive (and perfectly well-intended) conservationists accused me of trying to enhance my lot with the scientific community by increasing the size of a study area. They seemed unaware of the great significance of research at La Selva (both completed and prospective) for human welfare, and most of all, for Costa Rica, or that a great part of the value in protecting biological diversity comes from the knowledge that can be derived.

I want to leave two impressions. One is that getting this far has not been easy, and has involved unprecedented collaboration between conservation organizations, scientists, and two nations in particular. The other is that the saga will not end with the conversion of the Zona Protectora to Parque Nacional. Wonderful Costa Rica, the inspiration to so many for so many reasons, will shortly face a choice between importing timber, or invading protected areas–unless reforestation begins immediately. If this is the case for Costa Rica, how true it must then be that there are no truly protected areas anywhere unless the population/resource pressures are relieved.

La Selva is more than an exemplar of what is happening to the tropics; it is a keystone. For it is a fount of research and even more important, it is a key training ground for those who will add to this critical knowledge. Knowledge is indeed the key both to the intelligent use and protection of tropical biological systems. Attempts to bend tropical ecosystems to simple production systems are unsuccessful in many areas of the tropical forest regions of the world, unless large, expensive doses of fertilizers and pesticides are employed. The real solutions will be more complex and sophisticated ones that can be derived from the types of scientific knowledge that will flow from La Selva and the tiny number of other such sites of research.

Yet the significance of La Selva is even greater, for it is a key element in human efforts to explore the variety of life on earth. If the major part of biological diversity is destroyed, the biological sciences, with all their meaning for human welfare, will be forever stunted. Understanding of the life sciences will remain limited; perceived patterns and insights may in fact be incorrect for lack of critical evidence, and scientists may scarcely be able to know better. What chemist would have any patience for the notion of trying

to conduct that science with only half the periodic table—and for that matter, lacking the more interesting half?

Given the richness and complexity, the least explored part of the universe is the phenomenon of which we are a part, namely, life on earth. Major surprises of the last several years include organisms from ocean bottom rifts capable of living on the primary energy of the earth, bacteria able to live at temperatures in excess of the boiling point of water, and a wealth of insect life in the rainforest canopy that has tripled the estimate of the number of species on earth (Erwin 1983). It is not preposterous to anticipate many more surprises to come. Who would have predicted that the inspiration provided by the highly structured underside of the giant water lily of the Amazon would have led to the Crystal Palace, modern metal beam architecture, and provided the basis for the invention of the skyscraper? Did Eiffel know when he designed the market for the Amazonian rubber boom center of Manaus that all he really was doing was sending home a weak reflection of the giant water lily?

We are part of the most unusual phenomenon in the universe, and its fullest development is in the tropical forests. Surely the only sensible course, and in another sense the only moral course, is not to destroy the tropical forests, but to protect and explore them and in so doing truly celebrate life on earth.

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TROPICAL FORESTS: A STOREHOUSE FOR HUMAN WELFARE

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Although they cover only 7% of earth's land surface, tropical forests harbor an estimated 50% of earth's 5-10 million species. They are not only biotically as rich as all the rest of the world put together, they also represent the greatest repository of genetic resources for support of human welfare.

These genetic resources already make many contributions to our daily rounds. We benefit from tropical forest plants with our breakfast fruit and dinnertime dessert, with our wake-up cup of coffee and late-night cup of chocolate. Each time we obtain a prescription drug, there is one chance in four that our purchase owes its existence, in one way or another, to a plant or animal species from tropical forests. We further benefit from tropical forest species each time we apply a deodorant, an after-shave lotion, or a lipstick, each time we use cellophane or dynamite, each time we read a glossy magazine or mail a letter, each time we polish our furniture or our fingernails, and each time we wield a racquet or pull on our jogging shoes. We can even turn to tropical forests for future sources of energy; technology is now available to prepare "bio-crude" from plants at competitive prices, meaning that the day is coming when we will be able to replace petroleum with "phytoleum."

We enjoy these many products despite the fact that only one plant species in a hundred has been assessed by scientists for their economic applications. Thus there is vast scope ahead, provided the pharmacologist and industrial chemist can get to the forests before the lumberjack.

Tropical forests—considered here to be tropical moist forests (TMFs)—offer an extremely diverse stock of products. By virtue of their abundance of species, both plants and animals, they harbor an ultra-rich array of genetic

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resources among other so-called minor products that increasingly serve our needs through their contributions to agriculture, medicine, industry, and energy. This means that TMFs can supply a host of products to sustain the welfare of people around the world—products that, in their rich variety, far outstrip established products, namely hardwood timber, fuelwood, meat protein, and a few cultivated crops. Let us now look at each of the four main categories of "non-conventional" products in turn, through their contributions to agriculture, medicine, industry and energy. (This paper is based in part on Myers 1984; for additional detail, see IUCN 1985).

AGRICULTURE

TMFs contribute to modern agriculture mainly by supplying entirely new foods and improving the genetic makeup of existing crops.

TMFs already supply the origins of many staple foods, including cereals such as rice and millet, pulses such as peanut and mung bean, roots and tubers such as yam and taro, and other well-known items such as cassava, to name but the leading items (Chai et al. 1979; Rifai 1976; Williams et al. 1975). But the fact that these crops are so widely grown does not necessarily mean that they are the best crops. It is arguable that today's crops are accidents of history, and we grow them because they happened to be suited to cultivation by Neolithic man ten thousand years ago. A cornucopia of further foods waits to be investigated, many of which could become front-rank if adequate research and development are done.

As an example of a TMF plant that has recently emerged as a significant food source in many lands, consider the winged bean (*Psophocarpus tetragonolobus*), a plant from the forests of New Guinea (National Academy of Sciences 1975, 1982). This legume has long been known to forest tribes of New Guinea because of its nutritional content: it contains more protein than cassava, potatoes, and several other crops that serve as principal sources of food to many millions of people in the tropics. Indeed the winged bean offers nutritional value equivalent to soybean, with 40% protein and 17% edible oil, plus vitamins and other nutrients. It is coming to rank as the long-sought "soybean of the tropics," after a crash program of development and improvement during the past decade introducing it into human diets in more than 30 countries of the developing tropics.

Many other TMF plants feature nutritious leaves and other greenery. All in all, at least 1650 species offer vegetable-like materials (Herklots 1972; Martin and Ruberte 1979; Ochse 1977; Okafor 1980; Oimen and Grubben 1977; Villareal and Opena 1976). A good number of these species allow us to derive high-quality food in the form of leaf protein (Duke 1981; Mohan and Srivastava 1980; Pirie 1975).

Extensive as are these sources of new TMF vegetables, probably the greatest scope for new foods lies with fruits. Temperate-zone forests have yielded only about 20 major fruits, whereas TMFs feature at least 250 fruits that are enjoyed locally. In New Guinea alone, 251 tree species bear edible fruits, yet a mere 43 have become established as cultivated crops, and only about one dozen reach the marketplace (Jong 1979). There could be as many as 2500 fruit species in TMFs suitable for human consumption—yet of these, only 250 are widespread, 50 are well known, and a mere 15 rank as major commercial species (Nagy and Shaw 1980; Samson 1980).

A number of natural sweeteners are also available. In the wake of the cyclamate and saccharin controversies, there is urgent need for an alternative non-nutritive sweetening agent, i.e. one that does not add calories to our diet and centimeters to our waistlines. We now consume 100 million tons of sugar worldwide each year, or an average of 20 kilograms per person, and an average of 45 kilograms in many developed nations—much more than is good for human health. The pigments of many TMF plants, such as carotenoids in sweet-tasting fruits, attract birds, insects, and other herbivores; for the most part, they are not toxic to mammals, including humans. Certain ones contain natural sweeteners that comprise protein compounds rather than glucose, fructose, sucrose, and other sugars; these protein sweeteners are 1000 times sweeter than sucrose, and at least 300 times sweeter than saccharin. In the TMFs of West Africa, there are the so-called miracle fruits, *Synsepalum dulcificum*; the serendipity berry, *Dioscoreophyllum comminsii*; and the katemfe, *Thaumatococcus danielli*. The katemfe is now marketed by the British sugar corporation Tate and Lyle Limited, and already established in Japan, where it is used in such diverse products as candies, chewing gum, salad dressing, coffee drinks, soups, jellies, pickles, frozen desserts, fish and meat products, and table-top sachets (Duke 1983; Higginbotham 1979; Inglett 1981).

In a number of countries, wild meat serves as an important item in local people's diets (Ajayi 1979; DeVos 1977; Sale 1983). In Nigeria, humans derive a renewable harvest of almost 100,000 tons of animal protein from creatures such as grass-cutters (giant rats), small antelopes including bushbuck and duiker, and sundry monkeys. On average, this wild meat constitutes one-fifth of all animal protein in Nigeria's TMF zone. In Zaire, similar animals contribute almost 27% of all animal protein, and in Cameroon, Ivory Coast, and Liberia, as much as 70%.

Moreover, there is much opportunity for similar sustainable exploitation of TMF mammals in other parts of the world. In TMFs of tropical South America, for example, the tapir, agouti and paca among other rodents, plus peccaries and various monkeys, are all harvested for meat. In two separate sectors of Peruvian Amazonia, rural-dwelling people depend on wild meat for

at least 80% of their animal protein, with offtakes as high as 240 kg per square kilometer, and a marketplace value equivalent to US $440 (Paucar and Gardiner 1981). Were the harvest to be systematized, and expanded to include birds, fish, and turtles (see below), the minimum potential value could be increased to at least $4,000 per year. Were the harvest to include caimans for their hides, plus primates for biomedical research, a single square kilometer could, through careful management, yield an overall self-renewing harvest worth as much as $24,000 per year—a good deal more than commercial logging now offers.

Other TMF species, apart from mammals, can serve the same purpose. In Amazonia, seven species of river turtles could, if properly managed, become a sustainable source of high-grade meat (Mittermeier 1978). Turtles feed readily on aquatic plants of all types; they survive temporary food shortages at the end of the dry season without adverse effect; they have low metabolic rates, so they do not become nearly so hungry as warm-blooded creatures; and they appear to need less living space than birds and mammals. According to theoretical calculations, a one-hectare lake of turtles could produce over two tons of meat per year, by contrast with the 50 kg of beef from one hectare of average cattle pasture in the humid tropics.

TMF species also contribute to the improvement of established crops. Many modern food crops require constant infusions of genetic variability in order to resist emergent types of diseases and pests, environmental stresses and the like, as well as to increase productivity and nutritive content. In many cases, the germplasm material comes from wild plant relatives. During the past few decades, genetic resources from TMFs have saved a number of important crops, including sugar cane, coffee, cocoa, and banana (Carlson 1980; Frankel and Hawkes 1974; Harlan 1975; Hawkes 1978; Myers 1983). In the case of sugar cane, plantation growers in the southern United States suffered from a mosaic virus in the mid-1920s, eliminating three-quarters of the 180,000-ton-per-year crop (Harlan 1975). Fortunately, mosaic-tolerant varieties of sugar cane were found in a wild species of secondary forests in Java. More recently, further wild types of sugar cane have supplied resistance to red rot, gummosis, and other pathogens. A parallel story can be told for coffee (Ferwerda 1976). As for cacao, wild germplasm is found in the species' native habitats in western Amazonia, and in relict patches of forest in the Pacific coast zone of Ecuador. In the latter site, one particular variety of the cacao plant has now been reduced to just a few surviving individuals in the 1.8-square-km Biological Reserve at Río Palenque, a type of cacao with better taste and other virtues than is found in almost all other gene pools of wild cacao (Gentry 1982).

Yet a further illustration of wild-gene support from TMF plants involves the recent discovery in a small patch of montane forest in south-central

Mexico of a weedy-looking form of wild teosinte (*Zea diploperennis*), a close relative of modern corn (Iltis et al. 1979). A perennial form, it could, through cross-breeding with conventional annual varieties of corn, eliminate heavy seasonal costs of plowing and sowing. Moreover, being native to cool moist environments of its montane forest habitat, the wild variety could allow corn cultivation to be expanded into environments that have hitherto remained closed to it, expanding the range of modern corn by at least one-tenth, or some 40 million tons a year. The wild corn also offers resistance to seven major diseases (Nault and Findley 1981). Total benefits for the global corn industry could eventually be measured in billions of dollars per year (Fisher 1982; Myers 1981).

TMFs can further support modern agriculture by supplying materials to help control the many insect pests that account for the loss of 40% of all food grown around the world each year. A sound way to control insect pests is to exploit chemicals from plants that have developed mechanisms to resist insects. The finest source of such plants lies with TMFs and their exceptional variety of plant forms that have co-evolved in equilibrium with associated insects (Gilbert and Raven 1980; Janzen 1975; Metcalfe 1977). TMF plants constitute a vast storehouse of chemical substances for defense against insects—not only biocompounds that serve as insect repellents and toxicants, but feeding deterrents of various sorts, inhibitors of insect growth and development, and the like. All these compounds are biodegradable, i.e. they do not accumulate in organisms, and thus do not contribute to the environmental problems associated with synthetic chemical pesticides. Notable examples of these compounds are the pyrethrins, from chrysanthemum-type plants, and the rotenoids, from roots of TMF legumes. In addition, insect pests can be tackled through natural enemies, in the form of predators and parasites, especially from TMFs where natural enemies exist in greatest abundance and diversity (Batra 1982; Clausen 1978; Coulson 1981).

Finally, domestic livestock can be upgraded through genetic resources from wild creatures of TMFs (National Academy of Sciences 1983). For example, the kouprey (*Bos sauveli*), a cow-like creature of TMFs on the Thailand/Kampuchea border, has potential for cross-breeding with the humped zebu cattle of southern Asia, as the kouprey appears immune to rinderpest. Other wild bovids of TMFs in Southeast Asia that could likewise upgrade cattle husbandry are the so-called "dwarf water buffalos," the tamarau (*Bubalus mindorensis*) and anoa (*Bubalus depressicornis*). In addition, TMFs of Indonesia harbor the babirusa (*Babyrousa babyrussa*), a distant relative of the common pig that seems to be a primitive ruminant. Because of its capacity to convert rough forage into good meat, it could not only serve as a new source of food in itself, but could enhance the productivity of the half-billion pigs around the world.

MEDICINE

Modern pharmacopoeias benefit markedly from TMF plants. Indeed TMFs represent earth's main repository of naturally occurring drugs, with a greater percentage of alkaloid-bearing plants than any other biome (Levin 1976; Raffauf 1970). Plant alkaloids with notable medicinal applications include cocaine, reserpine, quinine, ipecac, caffeine, nicotine, and colchicine.

In northwestern Amazonia alone, over 1300 plant species are employed by Amerindians as medicines and drugs of one sort or another (Schultes 1980). In Southeast Asia, traditional healers use some 6500 plants as treatments for malaria, stomach ulcers, syphilis and assorted other disorders, also as sedatives and emetics (Perry 1980). A good number of these ethnobotanical materials yield exceptionally promising compounds for use in modern drugs and pharmaceuticals (Duke and Wain 1981; United Nations Industrial Development Organization 1978; Von Reis and Lipp 1982; Wagner and Wolff 1977). For instance, at least 1400 plant species of TMFs are believed to offer potential against cancer (Barclay and Perdue 1976; Cordell 1978; Douros and Suffness 1980; Duke 1982; Spjut and Perdue 1976). In 1960, a child suffering from leukemia faced one chance in five of remission. Now, thanks to two drugs developed from a TMF plant, the rosy periwinkle (*Catharanthus roseus*), the patient enjoys four chances in five (Taylor and Farnsworth 1975). Worldwide sales of these two drugs now total $130 million per year (Brooke 1978; Myers 1983). TMF plants offer significant contributions, whether actual or potential, to other medical problems, notably hypertension, blood-pressure problems, and birth-control (Altschul 1977; Lewis and Elvin-Lewis 1977; Soejarto et al. 1978).

As a measure of our present benefits from TMF plants for medicine, we reckon that when we take a medical prescription to our local pharmacy, there is one chance in four that the medication we purchase owes its origin to startpoint materials from TMF plants (Farnsworth and Morris 1976). The commercial value of these products worldwide now tops $10 billion a year; when we add in non-prescription items and pharmaceuticals, the amount doubles (Myers 1983, 1984).

INDUSTRY

TMFs offer a broad array of materials that meet the needs of innovative industry. These materials include essential oils, latexes and other exudates, gums, resins, terpines, volatile oils, tannins, sterols, waxes, esters, acids, phenols, alcohols, edible oils, rattans, bamboos, flavorings, sweeteners, spices, balsams, and dyestuffs, among a host of other materials (Duke 1981; Goldstein 1981; Gottlieb and Mors 1980; Lipinsky 1981; Princen 1979; Pryde et

al. 1981). These materials serve in the production of many items used in our daily rounds, including foods, polishes and varnishes, sizings, lubricants, etc. Fibers and canes, in the form of rattans, supply wickerwork furniture. Essential oils contribute to mouthwashes, deodorants, instant coffee, and cough pastilles, among a host of other items. Edible oils—used not as food additives but for industrial applications—appear in our everyday lives in the form of detergents, candles, emollients, lubricants, cellophane, and explosives. Exudates, notably gums, resins, and latexes, serve us each time we seal an envelope or affix a postage stamp, hit a golf ball, or chew gum. Waxes support our lifestyles each time we read a glossy magazine or take a carbon copy of a credit-card slip. They even serve as a binder in manufactured dog foods. Tannins and dyes appear each time we get out our Gucci accessories or pull on our jogging shoes.

In particular, the global chemicals industry, worth more than half the global armaments industry and thus truly big business, is becoming concerned that petrochemicals with their soaring costs will cause plastics, among other petrochemical products, to be priced beyond reach of the consumer. So chemical-industry leaders are seeking alternative supplies of organic raw materials—and they are turning especially to the phytochemicals of TMFs. Technology is now available to manufacture 95% of synthetic products from selected plant materials, not only plastics but artificial fibers, adhesives, furfural, formaldehyde, polyisoprenes, and surface coatings.

ENERGY

The contribution of TMFs to the energy sector in the form of fuelwood is all too apparent. But since fuelwood is an established product of TMFs, we shall not go into it further here. Rather we shall look at some pioneering ways for TMFs to contribute to energy supplies.

There is now the prospect that TMF plants can generate vegetation of sorts that can be readily converted into "green gasoline" and other types of energy. Bear in mind that photosynthesis gave rise to startpoint materials for geologic formation of oil, coal, and natural gas. It would be a giant advance for us if we could eliminate the millions of years that have transformed ancient green plants into fossil fuels, and instead to harvest the stored solar energy of present-day plants. Indeed, it is photosynthesizing plants that offer by far the simplest way for humankind to collect solar energy, and then to process the vegetative material into "biocrude" (Bente 1981; Hall et al. 1982; Office of Technology Assessment 1980).

Several technologies are available to convert biomass (large amounts of it, assembled at a single location) into fuels, whether of liquid, gaseous, or solid form. Among principal modes are biomethanation, fermentation, and

pyrolysis. The key factor lies with those plants that generate enough vegetative material in short order. The present front-rankers are starch crops, such as corn and cassava, or sugar crops, such as cane and beet. But a good number of TMF plants are similarly suitable. The best known is probably the giant ipilipil (*Leucaena leucocephala*), an evergreen legume native to Central America, and now one of the most widespread and versatile plants on earth (National Academy of Sciences 1977). Generally speaking, one ton of pyrolyzed wood can yield some 12 liters of methanol (methylated spirit), 35 liters of wood oil and light tar, 330 kilograms of charcoal and coal-like residues, and 140 cubic meters of gas, plus a number of by-products of industrial value (Earl 1975; Inman 1977; Tatom 1981). A 12,000-ha plantation of ipilipil can generate an estimated energy equivalent of one million barrels of oil a year. What will count for the future of ipilipil as an energy source is the extent to which plant breeders can improve the tree's genetic content; clearly a premium rests on selecting genetic strains from wild trees that are best adapted to "petroleum plantations." Equally important, plant breeders need to investigate other TMF trees that offer similar potential for ultra-rapid growth.

A number of plants yield hydrocarbons directly in that they produce hydrocarbons rather than carbohydrates in their tissues (Benedict et al. 1980; Calvin 1980; Jones et al. 1979). Several members of the family Euphorbiaceae produce significant amounts of milk-like sap, or latex, that is actually an emulsion of 30% hydrocarbons in water. These hydrocarbons are similar to those produced by the rubber tree, though of much lower molecular weight (in fact, of a weight order that is favored by oil engineers), and with a molecular configuration that resembles that of hydrocarbons in petroleum. *Euphorbia* hydrocarbons are even superior to those of crude oil, in that they are practically free of sulphur and other contaminants. Other species of *Euphorbia* from TMFs could prove to be leading candidates for "phytoleum." Similarly promising is a member of the legume family, *Copaifera multijuga*, a tree of Central Amazonia that can be tapped for its hydrocarbon fluid; the sap's makeup is so close to that of diesel fuel that it can be put directly into the tank of a diesel truck.

Finally, a TMF plant with a highly volatile oil that is best used not as a fuel for combustion engines but for household needs. Half a dozen stems of the "petroleum nut tree" (*Pittosporum resiniferum* of the Philippines) produce 300 liters of oil per year, for use in cooking, lighting, etc. The oil contains hydrocarbons of a type rarely found in nature, sometimes so flammable that when the nuts are freshly picked they can be lighted with a match. Fortunately the tree seems to thrive in secondary or disturbed forests, which means there should be plenty of opportunity to establish bio-fuel plantations without encroaching on primary forest.

OVERALL EVALUATION

These diverse products, known in forestry as "minor" forest products, can be proven not so minor. In Peninsular Malaysia, for example, lowland forests contain at least 1,283 non-timber plant species of identified use to humans, constituting roughly 16% of all native species in the Peninsula (Jacobs 1982). If we extrapolate from this data base, albeit a meager one, to other forests of similar sort, we may estimate that about one species in six could serve non-timber purposes of one kind or another. This means, in theory at least, that a minimum of 15,000 plant species in TMFs could offer potential to meet our material needs.

As for the economic value of these products, rattan exports from Indonesia are worth at least $55 million a year, leading to end-products with an across-the-counter value of more than $4 billion (Dransfield 1981). In addition, Indonesia's exports of citronella oil were worth $2.2 million in 1980; sandalwood oil, $1.7 million; patchouli oil, $11.6 million; and all essential oils, $21.1 million (Tcheknavorian-Asenbauer and Wijesekera 1982). Together with exudates and diverse other non-timber products, totalling 80,000 tons in all, Indonesia's minor forest products in 1980 earned $42 million. Moreover, these figures reflect only a crude minimum calculation of total revenues; many other products, categorized by Indonesia's statistical surveys under various commodity headings, would push the total a good deal higher.

For a more systematic and comprehensive assessment, let us look at India (Gupta and Guleria 1982; Pant 1977). In 1977 the total net revenue accruing to India's forestry sector, from all sources including commercial timber, amounted to $336 million. Of this total, minor forest products accounted for $134 million, or 40% (and their share of forestry exports, 63%). Since an estimated three-fifths of all minor forest products are used by local people, that is, they are consumed on the spot, they do not enter the cash economy, and hence are not incorporated into national accounting figures. This suggests that a realistic figure for the value of India's minor forest products would be more than $200 million. Among leading categories in 1977 were medicinals, drugs, and pharmaceuticals, worth $38.4 million; lac and lac products, $19.8 million; gums, resins, and balsams, $14.6 million; bamboos, $6.8 million; and essential oils, $5.9 million. Equally important, the rate of growth in revenues from India's minor forest products during 1970-77 amounted to 15.6% per year, way ahead of that for commercial timber. In addition, minor forest products were generating much employment, more than 70% of the 2.3 million man-years in the forestry sector overall. The true figure for employment, including those man-years not counted by official surveys, could have been as high as 4 million.

Policy Implications and Recommendations

This all leads to a number of important implications for forest policy, together with some recommendations for adaptive action, as follows:

1. In light of the many non-timber products that we already enjoy from TMFs and the many more that would surely become available if we evaluate their full potential, there is urgent need for research appraisals to assess the entire spectrum of non-timber materials available from TMFs, emphasizing key categories such as genetic resources and phytochemicals that contribute to agriculture, medicine, industry, and energy. As a measure of the long road that lies ahead, *and* of the possibilities awaiting us, scientists have documented only 20%, at most, of all TMF species, and they have conducted intensive investigations of only 1%.

Developing countries do not possess a fraction of the research resources necessary. So a major responsibility should fall on developed nations where a major incentive likewise lies, insofar as it is mainly developed nations that possess the research-and-development technology to exploit TMF materials.

2. There is also urgent need to undertake economic analysis of the entire range of material goods available from TMFs. We have a sound idea of the value of hardwood timber; we have too little grasp of the ultimate value of TMFs' many other products, even though it is now possible, by drawing on marketplace experience, to attempt minimum-value estimates. These estimates, however preliminary and approximate, should take explicit account of little-recognized products of TMFs, to adjust for the asymmetry of present evaluation procedures that highlight established products such as hardwood timber while virtually ignoring non-conventional products such as germplasm.

A few efforts at expanded cost-benefit analysis have been attempted (Carpenter 1982; Gregersen and Contreras 1979; Hufschmidt and Hyman 1982). Plausible as these attempts are, they tend to be limited not only in number but in scope: they do not match the nature and scale of the problem. The many fine-grain analyses of, for example, timber demand-and-supply trends should be complemented by equally rigorous analyses of the costs that may arise if TMFs, and their many non-timber products, continue to disappear. A widely documented assessment of TMFs' little-recognized products is now available (IUCN 1985).

3. What in all this should be the role of environmental organizations? Firstly, they can help to "spread the message" (see concluding statement under 2 above). Secondly, they can promote the concept of sustainable development in TMFs as "wise use"—a proposition that environmental organizations, before all other agencies in the conservation and development field, should promote with appropriate vigor. After all, development of TMFs, within a framework of sustainable outputs, can include genetic reservoirs as a

form of development that ranks alongside timber harvesting. A national park is as legitimate a "use" as a paperpulp plantation. In certain localities, "use" can entail outright preservation of forest ecosystems for scientific research, especially applied biology research as it relates to new ways for man to reap earth's natural bounty in TMFs with their abundance and variety of material products. Viewed from an overall perspective, we—conservationists, foresters, land-use planners, resource economists, political leaders—should expand our focus from the limited concept of "development of TMFs" to the much broader concept of "TMFs' contribution to overall development."

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COMPLEXITY IS IN THE EYE OF THE BEHOLDER

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Complexity in biological systems cannot be measured by the number of species present, even though this parameter is traditionally used as an intuitive measure of complexity. What matters in complexity is how many kinds of organisms a given organism recognizes in its interactions with those organisms. Likewise, what matters is the number of species that a species is linked to in the habitat, since this number determines in part how much of a change in one species will be perceived as a change by other species. These generalities are illustrated with examples from the saturniid moth caterpillars and their predators and parasites in a Costa Rican dry forest in Santa Rosa National Park. It is possible to conclude that, for example, to a foraging bird, a tropical habitat rich in caterpillar species may be no more complex than is an extra-tropical habitat poor in species; ten species of green and edible caterpillars may be perceived as identical to 100 species of green and edible caterpillars.

Complexity is also related to the number of links and demographic patterns in food webs that are affected by the removal of a link. Owing to evolutionary conservatism, traits are often retained long after the events that selected for them have disappeared. This type of complexity in food webs and time is illustrated by considering the ecological impact of extinction of neotropical dispersal agents. The Pleistocene extinction of the horse probably caused substantial changes in the demography of the plants whose seeds it dispersed, and this in turn should have affected the demographies of the other animals that were dependent on those plants, which should in turn have affected the demographies of the other plants those animals serviced, etc. The example is then carried further by viewing the seemingly unoccupied Australian dry tropics as in fact a landscape that has suffered mass extinction of species and habitats through 30,000 years of dry season burning by indigenous peoples. Its complexity is the most difficult of all to see.

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"Complexity" is often used to describe tropical forests. Its companion, great species richness, is used no less commonly. Just what is complexity? Is it in fact a long list of Latin binomials, the raw material for the trait of great species richness? As a tropical field biologist, my reply is that complexity is in the eye of the beholder. The length of a list of "species" in a habitat depends on who you ask. Furthermore, it is not so much how long is the list of species, but how the species interact that is the basis for biological complexity. A habitat whose vertebrates are six species of gazelles is likely to be less complex than one containing two species of gazelles, two species of large cats and two species of vultures. Again, how the parts interact may be very much a product of who is the beholder. There may be no interaction among three species of caterpillars eating three species of plants, but those three caterpillars may be very interactive parts of the diet of a bird that feeds on all three of them. Finally, the complexity of a tropical habitat is not something intrinsic to the site, but rather a delicate construction that changes as the ecological forces at a site change. These forces may no longer be visible to the beholder or even to the experimenter, but it is in the nature of nature that their impact on complexity is long-lasting.

THE SQUIRREL CUCKOO AS ETHNOZOOLOGIST

Santa Rosa National Park is 108 km^2 of dry tropical forest and abandoned pastures in northwestern lowland Costa Rica (Fig. 1). If we ask an insect taxonomist how many species of saturniid moth caterpillars (Fig. 2, and see figures in Janzen 1982a, 1985) occur in Santa Rosa, the reply will be "30 species" (Janzen 1982a), which is half as many as occur in all the U.S. and Canada (Hodges et al. 1983). Saturniids are the biggest moths in the world (Janzen 1984a), and are often called "giant silk moths" (e.g. Gardiner 1982); the cecropia, polyphemus, and luna moth are most familiar to North Americans (Ferguson 1972).

However, Santa Rosa is examined by more than insect taxonomists. The park is occupied by a healthy breeding population of squirrel cuckoos (*Piaya cayana*, Cuculidae; Fig. 3). These medium-size insectivorous birds are specialists at locating and preying on large caterpillars such as those in the Saturniidae.

If we ask an adult squirrel cuckoo how many species of saturniid caterpillars there are in Santa Rosa, it might reply "three kinds." First, there is the kind that when found is simply mauled and eaten or carried home to the nestlings. *Eacles imperialis, Rothschildia lebeau, Othorene purpurascens, Schausiella santarosensis* and *Caio championi* are examples from Santa Rosa. These large caterpillars (full-size *E. imperialis* caterpillars [Fig. 2a], weight 15-25 grams) are harmless to all vertebrate predators (though some are spiny

Fig. 1. Location of Santa Rosa National Park in northwestern Costa Rica. The volcanos that isolate the northwestern Pacific coastal lowland dry forest from the Atlantic rainforest lowlands are indicated by their specific names. The La Selva Biological Station, mentioned frequently elsewhere in this volume, is also indicated.

mimics of urticating caterpillars and therefore rejected by monkeys and perhaps by some other species of birds). They appear to escape mostly by being cryptic and by occurring as widely scattered individuals in the crowns of large trees.

The second kind consists of those caterpillars that are truly dangerous to vertebrates by virtue of extremely urticating spines (to a human, they hurt more than does stinging nettle) (Janzen 1984a,b). The squirrel cuckoo grabs one of these caterpillars (Fig. 2b) at the head with its bill and then bashes the caterpillar on a tree branch until it is quite dead. With death, the turgor

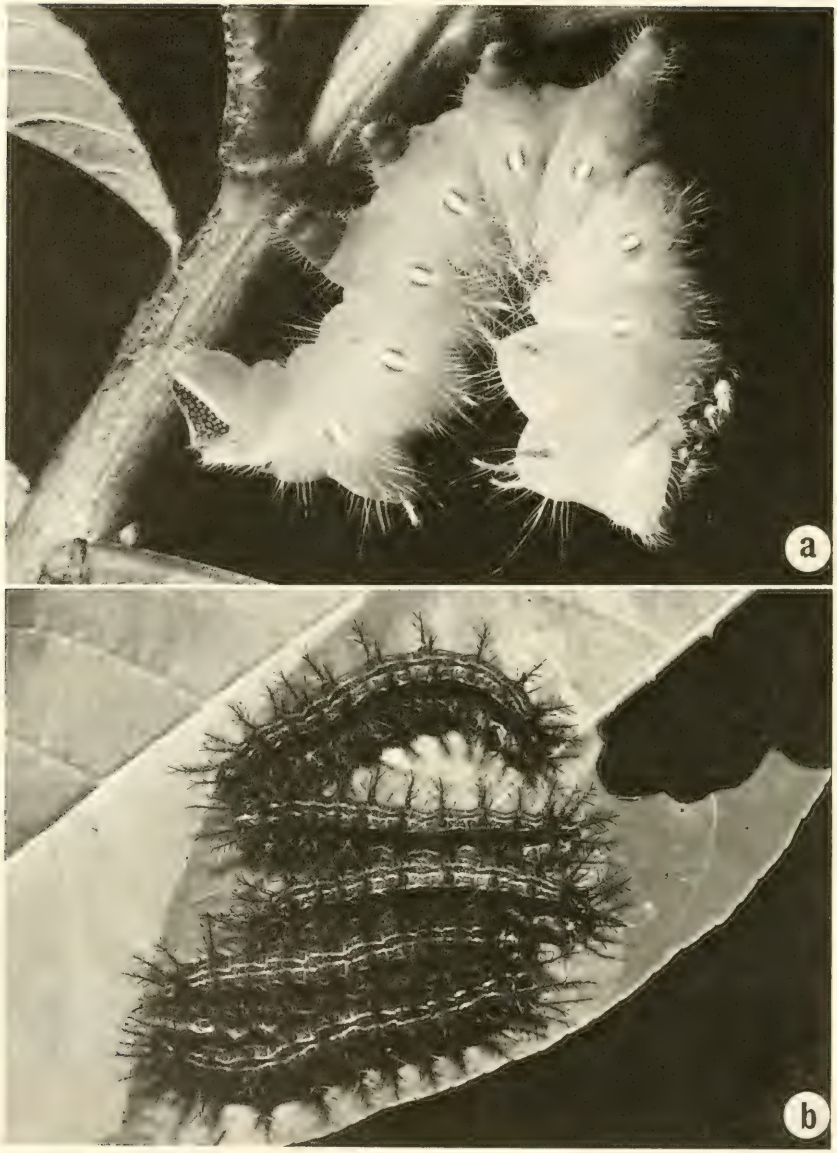

Fig. 2. a. Final instar caterpillar of *Eacles imperialis* (Saturniidae; 90 mm in length). b. Penultimate dark morph urticating caterpillars of *Hylesia lineata* (Saturniidae; 35 mm in length). Santa Rosa National Park, Costa Rica.

Fig. 3. Road-kill adult squirrel cuckoo (Cuculidae, *Piaya cayana*, 31 cm in length, Santa Rosa National Park, Costa Rica). Note the short, round wings and long tail—important features for agile and almost hovering flight in dense vegetation where it searches for caterpillars.

pressure of the body fluids declines and the urtication ability of the urticating spines (which are like liquid-filled syringes) is significantly reduced. The battered caterpillar is then swallowed entire. All hemileucine caterpillars at Santa Rosa (e.g. species of *Automeris, Molippa, Dirphia, Hylesia, Periphoba*) are of this kind. I do not know if the squirrel cuckoo is sufficiently deceived by the saturniid Batesian mimics of these urticating saturniid caterpillars (e.g. the harmless spiny caterpillars of *Ptiloscola dargei* and *Copaxa moinieri* [see figure in Batten 1984]) to process the mimics in this manner before eating them.

Finally, there is the kind of caterpillar that is found but rejected. There are only two saturniid Latin binomials in this category at Santa Rosa—*Arsenura armida* and *Rothschildia erycina*. I have watched adult squirrel cuckoos that were foraging for caterpillars hop within a few cm of large *R. erycina* caterpillars and simply ignore them. *Rothschildia erycina* caterpillars have the brilliant ringed color pattern of a coral snake (e.g. cover illustration of Janzen 1983a), as does *A. armida* (Janzen 1982a). There can be no doubt that the *R. erycina* caterpillars were seen and rejected, rather than simply overlooked. I have not yet witnessed a response to *A. armida* caterpillars, but I assume that these caterpillars are also seen and rejected. They occur in groups of hundreds of extremely ostentatious caterpillars within squirrel cuckoo foraging ranges but are not harvested by them. I assume that the squirrel cuckoo has the same

avoidance response as do two other species of Santa Rosa birds that eat large caterpillars, a kiskadee and a motmot: these two birds have been shown to be genetically programmed to fear and avoid the coral snake color pattern (Smith 1975, 1977). I assume that the squirrel cuckoo has the same avoidance response. I hasten to caution, however, that other caterpillar-eating generalist vertebrates do not categorize the Santa Rosa caterpillar array as does the squirrel cuckoo. For example, I have watched the large *Ctenosaura similis* lizards in the same habitat repeatedly consume the brightly colored coral snake look-alikes (*R. erycina*) that are rejected by the squirrel cuckoo.

In sum, the squirrel cuckoo thinks that there are only three kinds of saturniid caterpillars in Santa Rosa. If there were some species of saturniid caterpillars so cryptic that they were never noticed by the squirrel cuckoo, there would also be a fourth kind of caterpillar—but the bird could not know this and therefore would not include it in its reply to your questionnaire.

Squirrel cuckoos also eat species of caterpillars that are in other families of Lepidoptera. The bird's three kinds of caterpillars—those eaten, those processed and then eaten, and those rejected—each include large caterpillars of other families as well (Sphingidae, Noctuidae, Notodontidae, Oxytenidae, Megalopygidae, Geometridae). This suggests that even with 3000-plus species of caterpillars at Santa Rosa (Janzen, in press), our squirrel cuckoo would still at best tell us that there are only three species of caterpillars at Santa Rosa. Furthermore, a medium-size caterpillar-eating bird of a large state park in the central U.S. would probably also reply "three" (though its kinds might be defined by different boundary traits than would be the kinds recognized by the squirrel cuckoo, as in the case of the *Ctenosaura* lizard mentioned above).

However, not only vertebrates have opinions as to the number of kinds of caterpillars in Santa Rosa. There are, for instance, at least 40 species of parasitic wasps in the genus *Enicospilus* (Ichneumonidae) in Santa Rosa; there are at best 25 species of *Enicospilus* in all of the continental U.S. (I. Gauld, pers. comm.). *Enicospilus* wasps (Fig. 4) lay their eggs in caterpillars. The wasp larva develops within a caterpillar and consumes its body tissues. There are four widespread species of *Enicospilus* in the U.S., and each specializes in a different group of species of caterpillars (I. Gauld, pers. comm.). One, *E. americanus*, attacks only the larvae of saturniid caterpillars, but it attacks many species of them (e.g. Peigler 1985; Krombein et al. 1979). It sees many Latin binomials as a single kind of host.

In Santa Rosa, there are three species of *Enicospilus* that attack Saturniidae, and they attack three species of them. Each wasp species is specific to its own host species. Hundreds of rearing records in an ongoing six-year study of caterpillar parasitoids suggest that each wasp species attacks only one species of Santa Rosa saturniid. For example, one species of *Enicospilus* has been reared over 300 times from the caterpillars of *Rothschildia lebeau*

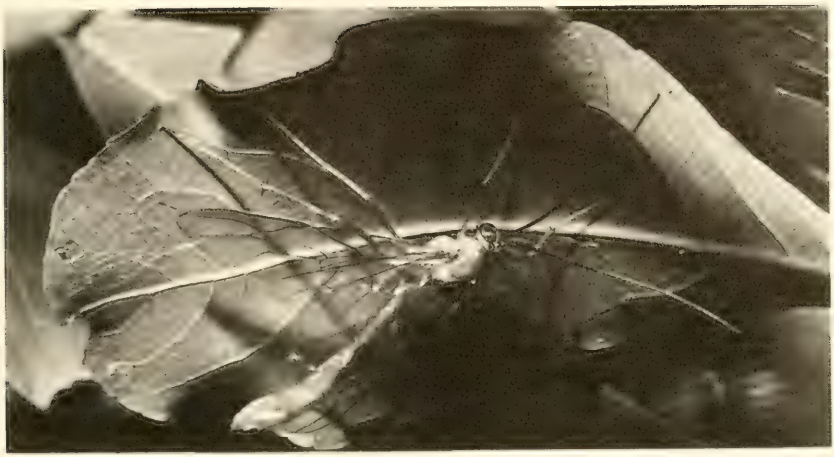

Fig. 4. Adult *Enicospilus* wasp (Ichneumonidae, 38 mm body length, Santa Rosa National Park, Costa Rica).

but never from the caterpillars of *Rothschildia erycina* (53 rearings of wild caterpillars to date), even when the two saturniid caterpillars developed simultaneously on the same individual host plant. In sum, each of these three species of *Enicospilus* that parasitizes saturniid caterpillars counts only one species and kind of caterpillar at Santa Rosa. I must be careful to note, however, that the wasp does not eat even a single Latin binomial. The moth, pupa, and eggs of the saturniids no more exist to the *Enicospilus* wasps than do all the other caterpillar species, leaves, hummingbirds, rocks, and snakes at Santa Rosa.

At this point you may conclude that each of the three species of *Enicospilus* that attacks saturniids in Santa Rosa views the tropics as having fewer kinds of caterpillars than does the single *Enicospilus* that attacks many species of saturniids in the U.S. However, recall the example of the squirrel cuckoo. One can argue that all attackable caterpillars belong to one kind and the remainder are non-existent. In this view, both the Santa Rosa *Enicospilus* and the U.S. *Enicospilus* think that there is only one kind of caterpillar in their habitats—the caterpillar in which they can oviposit.

This ecosystem tangle applies to all of the thousands of species in Santa Rosa and in the U.S. It is apparent why biologists are fond of using Latin binomials rather than biological perceptions as a standard unit of description. But this fondness has also led to a focus on species lists as descriptors of tropical habitats, rather than to a focus on the actual biological processes as descriptors. I might also note that *Homo sapiens* is particularly prone to act like a squirrel cuckoo or an *Enicospilus* wasp when it has to deal with biology that

is beyond its direct personal perception. Botanists are forever speaking of the biology of this or that species of plant, when in fact they ignore the seeds and seedlings and really are concerned with adult plants. Lepidopterists commonly think only of adult butterflies and moths when they speak of Lepidoptera. Ornithologists virtually never count the eggs in nests as part of a bird population, and if a species is territorial, they often ignore the adults that do not hold a territory.

But then does it really make no difference to the squirrel cuckoo that there are 3000-plus species of caterpillars in Santa Rosa? Does it not matter if an edible kind is made up of one or many Latin binomials? Does it matter to an *Enicospilus* if its host is made up of one or twenty species? It does matter, but putting numbers on how much it matters requires a knowledge of natural history much greater than we have at present.

For example, as the density of an *Enicospilus* single species of host declines, so also may decline the number of caterpillars that a wasp can find. However, if the wasp treats several species of caterpillars as a single kind, then when there is a decline in the density of one, others may serve as food in its stead. In short, the more species of caterpillars a wasp can use, the less likely is the wasp population to decrease following a reduction in density of one of them. Viewed the other way around, it matters to a caterpillar just how many other species of caterpillars one of its parasites feeds on. The more species of caterpillars fed on by one of its parasites, the less likely is a depression of caterpillar density to be reflected in a later depression in the percent of parasitization of that caterpillar. Finally, it is evident that the more different are the biologies of the hosts used by one wasp species, the greater will be the probability that a change in density of one host will not be synchronized with a change in the density of another host species.

And the squirrel cuckoo is in exactly the same situation as is the parasitic wasp. However, at a minimum, a female wasp only has to find two individual host caterpillars to replace herself. Owing to mortality of her offspring, she generally has to find more—perhaps even several hundred more since she can lay that many eggs. The female cuckoo, weighing several thousand times as much as does the 3-4 cm long wasp and living many years instead of a few weeks, has to find tens of thousands of large caterpillars to replace and maintain herself (the female wasp eats only flower nectar). Small wonder that the squirrel cuckoo does not specialize in foraging on the caterpillars of one or even a few Latin binomials.

It should now be clear that the complexity of a habitat is not measured in the simple length of the list of its Latin binomials. What matters to an insect or bird is how many species of caterpillars it pools as one kind, rather than how many Latin binomials there are overall. What matters is whether

the wasp can use or persist on one or two or three species of saturniid caterpillars, not whether there are 3000 species of caterpillars in the habitat. What matters to a saturniid caterpillar is not how many caterpillar species are in the habitat, but rather how many of those Latin binomials are supporting carnivores (predators and parasites) during the time when the caterpillar is scarce and how many Latin binomials are a food base on which the carnivores build up populations that later wreak havoc on the caterpillar population. In other words, 29 species of sympatric saturniid caterpillars may be as dangerous to a *Rothschildia lebeau* caterpillar as would be only one other species of saturniid caterpillar that is much loved by squirrel cuckoos, very common, and not prone to fluctuate in numbers.

THE FRUITS THE MEGAFAUNA LEFT BEHIND

As alluded to in the previous section, complexity may also be measured by the number of connections between an organism and the other organisms along the food chain. This may be dramatically illustrated by asking how far along in the food chain are the effects felt if a member of the food chain is removed. This experiment has been performed for us more times than we might like in humanity's frantic rush to destroy the tropics, but one case has an instructive special twist to it.

Ten thousand years ago, and for at least 3 million years before that, horses and numerous other large herbivorous mammals (the herbivorous megafauna) browsed, grazed, and harvested fruit over Central America just as they did in North America and others did in South America (Janzen and Martin 1982). The first wave of human hunters eliminated nearly all of these animals (Martin 1984). The Spaniards brought one back to us, the horse (horses originated in the New World and moved across the Bering Straits into the Old World before the Pleistocene hunters got to the New World by the same route).

This Spanish gift from the past found the fruits of the jicaro tree (Figs. 5-7, *Crescentia alata*, Bignoniaceae, the catalpa family). It found them in those few habitats where a megafauna-dispersed tree can grow without its dispersal agents and/or around Indian villages where the 5-20 cm diameter hard (Janzen 1982b,c) and spherical jicaro fruits were used for food and bowl-like utensils. The Spanish riding horse cracked the hard shells of the jicaro fruit with its incisors (Fig. 6), swallowed the seed-rich and molasses-rich pulp with little chewing, and defecated viable seeds far and wide in many habitats (Janzen 1982b,c).

Jicaro spread and became a widespread tree once again—the Spaniards had returned one of its original dispersal agents. Jicaro enjoyed 400 years again as a widespread tree, so much so that it became widely regarded as a

Fig. 5. Jicaro tree (*Crescentia alata*, Bignoniaceae), more than 150 years old, growing in a very old pasture (Santa Rosa National Park, Costa Rica).

native (wild) part of the flora. But very modern man controls his horses. For example, in the mid-1970s he removed them from Santa Rosa National Park, for 400 years a cattle ranch, so as to create a more "natural habitat." The jicaro fruits lay rotting beneath the parent trees (Fig. 7), and seed dispersal stopped. Dry-season fires went uncontrolled, fueled by the ungrazed grass in abandoned pastures. Jicaro saplings and seedlings were killed by the fires and competition from 1-2 m tall grass, and repeated burning incinerated the adult trees. Santa Rosa still has some adult jicaro, but the population is

dwindling fast. In 1985, fire control was initiated and horses were again allowed to range free. This may reverse the decline of the jicaro population, but for the moment we can examine what it means for a forest/grassland mosaic to lose its jicaro trees.

When Santa Rosa had a free-ranging horse population and enough livestock to eat the grass back to a density where it was not a severe competitor with jicaro seedlings, jicaro was common and occurred on many drainage and soil types. Each adult jicaro tree makes huge flower crops during 1-2 week periods several times a year. Since many jicaro trees flower somewhat out of synchrony with each other, there are abundant jicaro flowers available for four or more months of each year. These flowers are heavily visited by long-tongued, narrow-faced, tiny *Glossophaga* bats (Howell 1983). These bats are the primary (if not exclusive) pollinators of jicaro flowers and obtain a major part of their food from jicaro flowers at certain times of the year. This implies that when the jicaro trees are eliminated, the *Glossophaga* bat density or seasonal presence will be substantially reduced.

Fig. 6. Adult range horse in the process of cracking a jicaro fruit prior to eating the pulp inside (Santa Rosa National Park, Costa Rica).

However, these flower-visiting bats are also major pollinators of other woody plants in Santa Rosa, such as *Bauhinia ungulata, Hymenaea courbaril* and *Ceiba pentandra* (cf. Heithaus et al. 1975). The removal of jicaro will lower the density of *Glossophaga* bats in the park, which will in turn reduce and alter gene flow, reduce fruit crop sizes, and eventually change the abundance of other species of trees. The latter two consequences may well reduce the density of some other animals, such as the agouti (*Dasyprocta punctata*). This large diurnal rodent, a major consumer of *H. courbaril* seeds and fruits in some habitats, is also a major disperser of the seeds of many species of trees at Santa Rosa (W. Hallwachs, pers. comm.). The interaction goes on and on.

There are many ways that a deleted interaction may be replaced by another interaction in nature. On the other hand, the loss of a single species of animal such as the horse may lead to a major ripple of quantitative and qualitative interactions through and beyond the habitat. Species such as the horse have been termed "keystone" species (Gilbert 1977), as if there were something special about them. However, it is becoming my experience that what is special about a keystone species is that an investigator happens to know enough about its natural history to see the changes that occur following its removal. All species that I have worked with in detail in the tropics have the property that the demise of one of them will cause an ecological ripple in the habitat. Some species make bigger ripples than do others when removed, but even this trait will vary in the eyes of the beholder. Yes, the addition or deletion of species only sometimes creates a ripple so great that *Homo sapiens* is directly affected through its physical needs, but it is not necessarily useful to put ourselves at the head of the importance list when trying to understand ecology.

THE GREAT AUSTRALIAN BARBECUE

The Australian dry tropics seem hardly to have been touched by the hand of man, as compared to the obvious and intense agricultural and wild harvest pressure that characterizes the remainder of the dry tropics. The Australian haven of about 2 million square kilometers of essentially unoccupied dry tropical forest seems at first glance to be a place where one can study the dry tropics as they once were.

Braithwaite et al. (in press) open their discussion of mammal assemblages with: "Tropics in Australia are extensive, relatively unpopulated and undisturbed." However, this is very much an illusion: the Australian dry tropics are one of the most severely human-influenced areas in the world's tropics. Yes, some faunal and floral species lists for dry tropical Australia are respectably long (e.g., Taylor and Dunlop, in press; Braithwaite et al., in press), but it is clear that these species are only remnants of what existed prior to invasion of Australia by hunting and firing humans.

Fig. 7. Accumulated rotting and (few) ripe jicaro fruits below a several hundred-year-old jicaro tree to which horses do not have general access: a small number of fruits have been opened by a single horse that passed through just prior to the photograph (Santa Rosa National Park, Costa Rica).

Human hunters and harvesters have been collecting food in dry tropical Australia for at least 30,000 years and probably for 10-50 thousand years before that (e.g. Merrilees 1968; Gill 1975; Kershaw 1984; White and O'Connell 1983; Singh et al. 1981; Ingram 1985). Everything known of their hunting methods, and those of hunters in dry habitats elsewhere, suggests

that grass fires (Fig. 8) were major tools of the harvest (e.g. Stocker 1966; Singh et al. 1981; Ridpath 1977). At the time of European contact, the fires were widespread but patchy in thoroughness owing to their occurrence in the early rainy season, when the world is only heterogeneously dry (cf. Stocker 1966; Ridpath 1977; Stocker and Mott 1981; Mott and Andrew, in press; Braithwaite and Estbergs, in press).

Apparently the function of fire was that of concentrating game animals in unburned sites, producing patches of post-fire new sprouts that attracted game, aiding in game ambush, clearing out the understory for visibility and projectile passage (ever try to throw a boomerang in a forest?), and removing spear grass (*Heteropogon contortus*, a very annoying Australian grass whose seeds are dispersed by penetrating mammal fur and even skin). These fires burned relatively unchecked (small patches of forest were explicitly protected by aborigines) and a single fire could easily burn through thousands of square kilometers just as it does today. It is likely that much of dry tropical Australia was burned in most years. Catling and Newsome (1981) have productively deduced that such fires should have selectively eliminated some species of vertebrates and altered the geographical demography of others. Likewise, experimental burning in Australia (e.g. Unwin et al., in press) is making it quite clear that tropical rainforest or dry forest will be replaced by eucalypt-forested grasslands under ordinary burning regimes. For the purposes of this discussion, however, it is instructive to return to Guanacaste Province on the dry Pacific coastal plain of northwestern Costa Rica with the above fire story in mind.

When the Spaniards arrived in northwestern Costa Rica about 1523, all indications are that they encountered a forested landscape that was sparsely populated by shifting agriculturalists and patches of variously-aged secondary forest succession and uncut forest. The largely deciduous forest experienced a six-month rain-free dry season, just as it does today and as does dry tropical Australia (Taylor and Tulloch, in press). During the following 450 years, European agriculture (and livestock-culture) cleared ever more extensive patches of forest. By 1940 most and by 1977 all of the area was officially viewed as free of forest (Sader and Joyce 1984). Where the cleared land was not used for fixed-field agriculture, it was burned more or less annually to convert it ever more thoroughly to grassland. African grasses such as *Hyparrhenia rufa* (Pohl 1983) were introduced to complete the conversion into pasture (Parsons 1972). The more fire, the more complete the conversion. The more complete the conversion, the more easily and thoroughly the habitat is burned. This lamentably self-reinforcing process has occurred throughout Central America.

Start with a dry and largely deciduous forest, make some clearings, and burn them annually. The clearings spread as the fire eats into the margins.

Fig. 8. a. *Eucalyptus*-clothed grassland prior to dry season fires. b. *Eucalyptus*-clothed grassland immediately after a dry season fire. Both photographs taken 30 m apart in mid-August, 1985, near Katharine, Northern Territory, Australia.

Within a few hundred years on ranches of several hundred km^2 (large enough that there are large expanses of vegetation unbroken by barriers of roads and croplands), the final result is a grassy plain. This plain is, however, dotted with forest fragments associated with habitats that are difficult to burn (marshes, cliff faces, spits of land between river forks, river banks, hills surrounded by rock faces deep ravines, rock outcrops, etc.). In Guanacaste Province, the only tropical habitat that I have watched carefully for a long time (24 years), these tiny habitat fragments (Fig. 9) are still in the process of losing species because of their small size. They are also still losing species because of the long-term persistence of root stocks remaining from the original forest; these plants take tens to hundreds of years to die out of habitats that cannot support them as breeding populations. These habitat fragments take time to lose many of their species because the loss does not occur until an exceptionally dry year, in which the usually unburnable site becomes burnable. At present, the tiny forest fragments (a few hectares to much less in size) contain approximately 20% of the original dry forest flora and fauna that once occupied Guanacaste. This is an overall figure. The species of plants, insects, and other animals have been extinguished differentially, since they have different needs, inter-fragment mobility, ability to colonize and recolonize fragments, etc. All of the large vertebrates and many of the large trees are gone from these fragments. Some herbs, vines, and fast-growing small trees are more common than they were in the original forest; these are among the species commonly viewed as roadside and fencerow weeds.

Dry tropical Australia has been treated like Guanacaste, but for 30,000 years. The tiny pieces of closed canopy or "monsoonal" dry forest scattered through Australia's dry tropics are the true remnants of what was once virtually the entire forest cover of an area as large as a quarter of the United States. The habitat ocean surrounding these forest bits is in fact an enormous undulating plain of largely native grasses. However, this habitat is not generally perceived as grassland by Australian biologists because viewed laterally, it looks like a "forest." That is, when you look at it, you see a lot of trees (Fig. 8). Viewed from above or below, Australia's (eucalypt) forests are just grassy plains dotted with amazingly fire-tolerant *Eucalyptus* trees (and their relatives). The trees are spaced far enough apart that direct sunlight penetrates to ground level in sufficient quantity to support a dense stand of grassy fuel.

The grass understory occurs even when large adult trees are as abundant as they are in a Central American dry forest. This begs the question of why eucalypt crowns do not close up the canopy, grow out to fill in the space between them. A similar question is why it is that within a eucalypt crown the leafing is not thorough enough to form a solid barrier to sunlight, as is the common case with dry forest deciduous trees when they are in leaf in the rainy season. It may be that the eucalyptus tree crown is evolutionarily

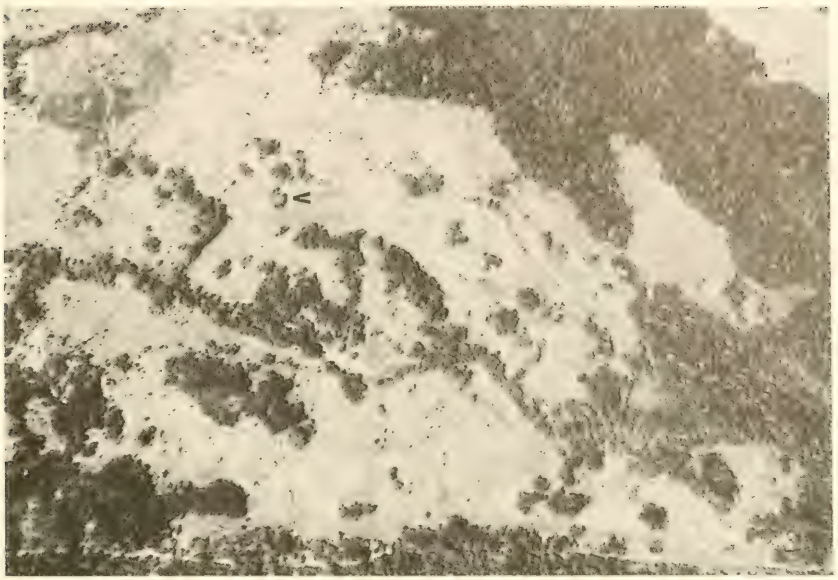

Fig. 9. Aerial view of several hundred-year-old pastures in Santa Rosa National Park. All of the light-colored area is jaragua (*Hyparrhenia rufa*) grass monoculture that was burned almost annually up through the 1984 dry season. Forest and forestlets are variously aged secondary succession that were being eradicated before the fire was halted. Arrow indicates a forest island under a single large guanacaste tree (*Enterolobium cyclocarpum*) whose crown is 40 m in diameter. Park entrance highway (two-lane) passes along base of photograph and center is Presa Pinuela. January 1985, Santa Rosa National Park, Costa Rica.

designed to let the heat from a grass fire pass quickly through, rather than form a tent to trap rising hot air that would kill branches and leaves. Equally, concentrations of individuals may be thinned by the lethal effect of their combined crowns accumulating hot air rising from the burning grass below. Many of the other species of trees that co-occur with *Eucalyptus* in frequently burned areas have deciduous crowns at the time of fires, stand far apart, and/or have very diffuse crowns.

There are many species of *Eucalyptus* trees in the dry Australian tropics (accompanied by the equally species-rich sister genus *Melaleuca* in the Myrtaceae, and the unrelated species-rich legume genus *Acacia*). If a fire-rich habitat is only 30,000 years old, are we to guess that the trees that occupy most of the habitat have speciated in this short time? Perhaps, but it is not necessarily so. The fire-resistant Myrtaceae could be serendipitously fire-resistant

and have been much older occupants of dry forest unburned habitats with a high frequency of disturbance (landslides, cliff faces, erosion ravines, marsh-stream-river-flood plain banks, heavily browsed/grazed areas, hurricane impact areas, etc.). Some species could even have been selected for fire tolerance in areas with exceptionally frequent lightning fires at the beginning of the rainy season (end of the dry season). But whatever habitats the fire-resistant *Eucalyptus* occupied originally, owing to their high fire tolerance they undoubtedly underwent an explosion in population size and geographic coverage when the original human occupants of dry tropical Australia began their burning regime.

The original occupants were, above all else, hunters and gatherers. In the Neotropics, the first waves of Neotropical hunters eliminated the bigger and slower of the Neotropical herbivores (Martin 1973, 1984) (and caused their predators and scavengers to starve; Janzen 1983b). The original human invaders of Australia did the same (Martin 1984). They certainly had a diverse fauna of large animals to hunt (Murray 1984) and those animals are no longer with us. It is not hard to imagine that the removal of these large animals reduced the frequency and extent of small-scale vegetation disturbance (leading to a more homogeneous fire regime) and reduced the dispersal of dry-forest tree seeds (leading to slower reinvasion of sites that were occasionally cleaned of their plants by exceptional fires). Australia also went through periods of climatic changes during this time. Habitats move, fragment, and coalesce as the climate changes. The movement of seeds by animals is an integral and important component to this habitat movement, and thus an important part of whether a climate change leads to species or habitat movement or to species or habitat extinction.

But then, enter the Europeans as a major agricultural force between 1800 and 1900 (depending on where you are in Australia, they and their influence on the fire regime arrived at different times). Aside from largely eliminating the original inhabitants and therefore indirectly eliminating their practice of burning early in the dry season, the Europeans were interested in raising cattle. And to do this, late dry season fires seemed best because they yielded a dry season harvest of green sprouts. Additionally, once the traditional early dry season fires were gone, the tinder-box nature of the habitat by the end of the dry season led to rapid and thoroughly widespread fires from accidents, ranches, or lightning. A small patch of deciduous dry forest that would be protected by a moist area or rocky outcrops from a weak fire early in the dry season will often be overrun by a raging fire late in the dry season.

The consequence of the shift in fire regime has been dramatic. The original eucalypts still stand over their grassy plain, but their recruitment is severely limited. Annual fires in the late dry season repeatedly eliminate all

but the most robust adult trees, and even these eventually succumb. Where grazing is severe enough to reduce grass fuel to non-inflammable levels, the eucalypt seedlings and sucker shoots are also eaten, and introduced grazing-resistant woody plants invade the forest understory. One day, within 100 years or so, Australians are going to wake up to find that almost overnight their dry tropical eucalyptus forests have been converted to treeless grassland habitats and deciduous forest scrub that is largely inedible to cattle.

What message does Australia's dry tropical forest story have for the understanding of tropical complexity? Australia is a marvelous example of how what you see in the tropics, species-rich as it may be, can still be but a tattered ecological remnant rather than an evolutionarily fine-tuned ecosystem millions of years old. Yes, there are hundreds of species of plants in dry tropical Australia. But this list is undoubtedly much shorter than it was 30,000 years ago, and it is going to get abruptly shorter as the European-style fire regime eliminates the last relict dry forest pockets.

Dry tropical Australia displays the striking ecosystem pattern of enormous areas covered with a few species-rich genera of grasses, trees, and shrubs, with a sprinkling of tiny refugee habitats containing many other species. However, it is likely that these plants did not come to have their current habitat status through evolution under a severe fire regime, but rather have been put in their places by a process of ecological fitting of fire-tolerant parts evolved in other disturbed habitats. Yes, dry tropical Australia has its spectacular vertebrates—goannas, wallabies, emus, bower birds, megapodes, cockatoos, magpie geese, etc. But this fauna is only a pale shadow of the marsupials that were as large as tapirs and rhinos, the huge ratites, giant kangaroos, etc., that early humans confronted. The impact of the extinct megafauna is still everywhere to be seen or tasted—thorns, burs, large fleshy fruits with woody or fibrous coverings around seeds, leaf defensive chemistry. Such an impact will require a special kind of reconstruction ecology to understand (e.g. Janzen and Martin 1982). This is an area of field biology very much in its infancy.

In sum, dry tropical Australia is complex and spectacular just as is (was) much of the remainder of the dry tropics. However, this complexity is only that which can survive the great homogenizers, fire and humanity. The regime of nearly annual burning and continuous hunting has been forced onto a complex tropical habitat. The effects have been indelibly recorded through extinctions and novel geographic distributions well before any evolution can occur to compensate for them. This type of complexity is also in the eye of the beholder, but the beholder is blind.

CONCLUSION

The tropics are a complicated environment. The direction and intensity of ecosystem processes are as much based on the idiosyncracies of the natural history of particular species as on major climatic and geological variables. One of those particular species is *Homo sapiens. Homo sapiens* has clearly beaten nature, and in doing so continues to convert habitats to the vegetation type that grows the resources to support a very large herd of human draft animals. May I only add that humanity has never displayed the trait of developing the brains of its draft animals. The bits of complex tropical nature that are still within the grasp of tropical peoples are perhaps this portion of humanity's last chance for mental stimulation extraneous to the pitiful stimuli offered by humanity itself. Life in a sugar cane plantation is not substantially improved by even two TV channels playing ten-year-old re-run movies from the U.S.

In the not-too-distant future, the most valuable pieces of real estate in the tropics will be the less than 10% that will be in national parks or other biological reserves. Can you imagine the intellectual response by Europe if 100 km^2 of Pleistocene forest and its animals could be made to reappear in central France? I do not intend to depreciate the complexity of human society. Rather I note that this complexity is only a very incomplete representation of what the human mind is capable of absorbing, using, and enjoying. The natural world, tropical or otherwise, at least allows the chance for a substantial increase in the completeness of that representation. Complexity is in the eye of the beholder, but there has to be something left to behold.

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I dedicate this paper to the right-minded persons in the Australian government who are willing to plan the long-term use and perpetuation of the Australian tropics, rather than simply to harvest them.

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LOCAL RESOURCE USE SYSTEMS IN THE TROPICS: TAKING PRESSURE OFF THE FORESTS

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By focusing research on indigenous and local agroecosystems, much information can be gained for the development of resource-conserving, ecologically sound land-use strategies that promote the sustained-yield management of land already cleared in tropical regions. By keeping the farmers on the land they already have, pressure can be taken off the limited forest reserves that still exist. A research approach that looks at the agricultural ecosystem (agroecosystem) will allow an agroecological focus, in order to examine impacts on the land in the context of nutrient cycles, crop and non-crop population dynamics, energetics, and other ecological concepts. Examples of such studies are presented from tropical Mexico and Costa Rica, including the corn/bean/squash multiple-crop agroecosystem, the tropical home garden agroforestry system with a diverse mixture of trees, shrubs, herbs, and vines, and an experimental bench-terrace-cropping system with mixed vegetables planted on the flat surfaces and a high organic-matter-producing grass on the slopes. The importance of the sustainability of the natural resource sector linked to the sustainability of the agricultural sector is stressed as an integral part of tropical forest preservation strategies of the future.

Throughout most of the tropics today, local or traditional knowledge continues to form the basic foundation of resource use systems. Such knowledge reflects experience gained from past generations, yet continues to develop in the present as the ecological and cultural environment of the populations involved goes through a continual process of adaptation and change. Studies of local resource use systems show us the value such systems have for contributing to the development of ecologically sound management practices

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that are understandable and acceptable to rural peoples in tropical regions (Klee 1980; Wilken 1977; Gliessman 1984; Altieri 1984). These systems often make use of locally available resources rather than relying on costly inputs imported from distant sources. They allow for the simultaneous satisfaction of local needs together with a significant contribution to demands on a larger scale. Most importantly, production takes place in ways that focus more on the long-term sustainability of the system, rather than an overemphasis on the maximization of yields. The ability of these systems to keep the land productive on a permanent basis reduces the need for the development of new lands. An agroecological approach to understanding how such systems function can provide information that can significantly contribute to relieving the current pressures on rapidly diminishing tropical forest reserves. Such a focus goes hand in hand with our efforts to preserve rainforest regions.

RESEARCH APPROACHES

By considering a particular resource management system as part of a larger ecosystem, the impacts of any particular management practice can be understood. An agroecosystem is defined as the particular farm unit, comprised of a set of inputs and outputs that are compartmentalized within an interacting array of biotic and abiotic components and managed for the purpose of supplying humans with needed food, feed, fiber, and fuel. Human impacts on the agroecosystem can be placed in the context of how nutrients enter, leave, or are recycled in the system. The population dynamics of crop and non-crop organisms respond to how we manage the system. We can examine the efficiency with which energy flows through, is stored, or is required for proper management. A thorough knowledge of the interplay between physical factors of the environment, their interaction with and modification by biological factors, and the incorporation of the management of particular resources for human use, can permit the establishment of an understanding of both the agroecological potentials and limitations of the region under study. The link to ecosystem studies can include the idea that many traditional or indigenous agroecosystems even "mimic" the structure and function of the naturally occurring ecosystems of an area. The examination of a variety of tropical agroecosystems has provided us with a valuable means of beginning to test these ideas. Part of this work has been carried out in the tropical lowlands of southeastern Mexico (Gliessman et al. 1981; Gliessman 1984), and is currently in progress in Costa Rica as part of the activities of the Organization for Tropical Studies and its courses in tropical agroecology (Jaffe and Gliessman 1986).

MULTIPLE-CROP AGROECOSYSTEMS

The use of crop associations or multiple cropping can take place in many cropping systems to great ecological and agronomic advantage (Amador 1980). More than one crop occupies the same piece of land either simultaneously or in some type of rotational sequence during the season. Production can be increased, more efficient use of resources takes place, and the land can be occupied productively more continuously. The importance of multiple cropping in the tropics is being recognized (Francis 1986), and the need for intensive agroecological studies of such mixed cropping has become more evident (Gliessman 1986).

Corn, bean, and squash polyculture (Fig. 1) has been the focus of many studies in Tabasco, Mexico (Amador 1980; Vandermeer et al. 1983; Gliessman 1984). Corn yields were stimulated as much as 50% beyond monoculture yields when planted with beans and squash (Table 1). Despite yield reductions for the two associated crop species, summed yields for the crops planted together were also higher than for an equivalent amount of land planted to the crops separately (over-yielding). The mechanisms of the stimulation of corn yields have been the subject of further study. On the one hand, it appears that beans in corn polyculture nodulate more and are more active in nitrogen fixation, and in making this nitrogen directly available to the corn (Boucher 1979). This led to observations of net gains of nitrogen in the agroecosystem biomass despite the removal of harvest yields (Gliessman 1982). These gains contribute to the long-term sustainability of resource use in the system. Squash, rather than being planted for fruit production, according to local farmers, was planted more for weed control. Thick, broad, horizontal leaves cast a dense shade that blocks sunlight and combines with leachates from the leaves that potentially inhibit weed growth through allelopathic interference (Gliessman 1983). Inhibition was determined through the use of leaf washings in germination and growth trials, as well as in pot experiments using the leaves as a mulch. An intercrop system can provide more microsite diversity for shelter or reproduction, as well as more variety of food sources, placing damaging insects at a disadvantage (Risch 1980) and promoting the presence of beneficial insects (Letourneau 1983). Every component of the system plays a role in maintaining productivity, the combined effects of which have been selected by the local farmers for many generations.

When faced with unpredictability of an environmental factor, such as rainfall, intercropping can prove useful. In Tabasco, I have observed interplanting of rice and corn, a practice which at first glance seemed inappropriate since the two crops have such different requirements. But

TABLE 1. YIELDS OF CORN/BEAN/SQUASH POLYCULTURE COMPARED TO MONOCULTURES PLANTED AT DIFFERENT DENSITIES
Cárdenas, Tabasco, Mexico (from Amador 1980)

	Monoculture Densities				*Polyculture*
	Very low	Low	High	Very high	
Densities of corn[a]	33,000	40,000	66,000	100,000	50,000
Yield (kg/ha)[b]	990	1,150	1,230	1,170	1,720
Densities of beans	56,800	64,000	100,000	133,200	40,000
Yield (kg/ha)	425	740	610	695	110
Densities of squash	1,200	1,875	7,500	30,000	3,330
Yield kg/ha	15	250	430	225	80

[a] Densities expressed as number of plants/ha.

[b] Yields for corn and beans expressed as dried grain, squash as fresh fruits.

considering that some years are wet and others dry (Garcia 1981), we found that in a wet year, the rice did best and in a dry year, corn did best. In moderate years it was possible to harvest both crops successfully (Gliessman, unpublished data).

Intercropping was frequently observed to include the use of non-crop plants or weeds (Chacon and Gliessman 1982; Altieri 1981). For instance, *Amaranthus dubius* is often intentionally left in corn plots to function as a trap plant for potential herbivore pests. Also, soil cultivation for the first 30 days following seeding of corn, then allowing the establishment of an almost pure ground cover of *Lagascea mollis*, will reduce damage to the crop from other weeds. In the former example, almost total defoliation of the *Amaranthus* was observed, with no damage on the crop. For the latter, few weeds were able to establish in association with the allelopathically active *Lagascea* (Gliessman 1983), but the corn was not harmed because it was beyond the sensitive early growth stages. The fact that the weed has 25-30% crude protein content and is useful as an animal feed adds to its utility (Losada, pers. comm.).

Fig. 1. (adjacent page). A view of the interior of a mature corn/bean/squash polyculture near Cárdenas, Tabasco, Mexico. Photo by S. Gliessman.

Local farmers also employ the use of cover crops in rotation with corn. A locally adapted variety of *Mucuna deeringianum* (locally called nescafe) is grown alternately with corn. It quickly forms a dense mat covering the soil, which, through both shading and allelopathy, inhibits weed growth, adds nitrogen to the soil, as well as important organic matter, and protects the soil surface. An annual, it dies back after five to six months, leaving the area ready for the next crop cycle. By growing this legume, farmers have reduced what is normally a five-to-eight-year fallow period to six months (Gliessman and Garcia 1979; R. Miranda, unpublished data).

TROPICAL HOME GARDENS

One of the agroecosystems that seems to be well adapted ecologically to the tropics, and in fact, has been proposed as a "mimic" of the tropical forest ecosystem (Ewel et al. 1982), is the home or kitchen garden system (Gonzalez 1985; Allison 1983). The value of such a system for tropical farmers is well documented (Anderson 1952; Kimber 1966; Anderson 1980). It is structurally diverse, with an overstory of trees and an understory of a mixture of herbs, shrubs, small trees, and vines (Fig. 2). This diversity permits year-round harvesting of food products, as well as a wide range of other products used by local people, such as firewood, medicinal plants, spices, and ornamentals. In an ecological analysis of home gardens in both lowland and upland sites in Mexico, it was found that even in a small area (0.3-0.7 ha), high diversity permitted a high degree of similarity between the managed agroecosystem and local natural systems. Relatively high species diversity for a cropping system was also achieved (Table 2). Undoubtedly, the great diversity of ages, height classes, uses, and locations in the gardens contributed to the high values.

In a home garden on the outskirts of Cañas, Guanacaste Province, Costa Rica, in an area of 1240 square meters, a total of 71 plant species were found (Fig. 3). The garden served as a source of food, firewood, medicine, color, and enjoyment for the household (Table 3). Some of the plant species served more than one function. The Shannon-Weaver species diversity

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Fig. 2. (adjacent page). Detail of a section of a home garden agroecosystem near Cañas, Guanacaste Province, Costa Rica. At least three layers of vegetation can be seen, excluding a tree overstory just out of view. Species visible from front to back include: sugar cane, taro root, papaya, and bananas. Ornamental plants in containers can be seen against the house and animal pens in the back. Photo by S. Gliessman.

TABLE 2. SPECIES TYPES AND CHARACTERISTICS OF HOME GARDEN AGROECOSYSTEMS AT LOWLAND[a] AND UPLAND[b] SITES (AFTER ALLISON 1983)

Characteristics	Cupilco	Tepeyanco
Average garden size	0.70 ha	0.34 ha
No. of useful species per garden	55.00	33.00
Diversity (bits)	3.84	2.43
Leaf area index	4.5	3.2
Percentage cover	96.7	85.3
Percentage light transmission	21.5	30.5
Perennial species ($\bar{X}$)	52.3	24.5
Tree species ($\bar{X}$)	30.7	12.3
Ornamental plants ($\bar{X}$)	7.0	9.0
Medicinal plants ($\bar{X}$)	2.0	2.8
Percentage introduced species	30.0	50.8

[a] Cupilco, Tabasco, Mexico.

[b] Tepeyanco, Tlaxcala, Mexico.

index (Southwood 1978) for the garden was 3.55, a relatively high value for an agricultural system. To a certain extent, plants were also distributed in the garden depending on the uses. Trees were concentrated towards the back of the plot (background of Figure 3), providing shade for the work area at the back of the house as well as stabilizing the border along a river-bank that parallels the back of the property. Annual food crops were concentrated towards the front of the garden in full sunlight. The ornamental species were clustered in beds or containers around the walls of the house and along the pathway leading from the front of the property to the house. Animal pens behind the house in the shade of the trees contained two pigs, a goat, and a guinea pig. An undetermined number of chickens freely roamed throughout the plot, as did several small dogs and two cats. Mango was the principal tree species, with corn, squash, beans, papaya, bananas, and

Fig. 3. (Adjacent page.) View of a home garden agrosystem near Cañas, Guanacaste Province, Costa Rica. At least 71 species of plants were found. Yuca, squash, beans, and corn are in the foreground; papaya, guava, and bananas midway; and mango trees in the back. Photo by S. Gliessman.

TABLE 3. NUMBER OF PLANT SPECIES AND INDIVIDUALS OF EACH SPECIES IN A HOME GARDEN AGROECOSYSTEM ON THE OUTSKIRTS OF CANAS, GUANACASTE PROV., COSTA RICA[a]

Plant uses	no. of spp.	no. of indiv.	% spp.	% indiv.
Ornamental	36	517	48	21.6
Food	26	164	36	68.2
Medicinal	6	1	8	1.6
Firewood	5	17	7	1.7
Animal feed	1	51	1	6.7

[a] Listed according to common uses. Total species and individual numbers are less than the sum of the columns due to the multiple function of some species. Adapted from: Carter, Bergmark, Dixon, Nagpala, Arias, and Gliessman, Field Problem Report of OTS 84-5, Tropical Agroecology (Jaffe and Gliessman 1986).

yuca (cassava) playing the most important roles in food production. The man of the household was employed full-time in the nearby town, so the garden played a supplemental role in the family economics. Additional studies of sociological characteristics of the family and its home-garden are needed to understand further the structure and diversity of the garden.

Home gardens are variable in size and design. They respond to local variations in soil type, drainage patterns, cultural preferences, economic standing of the family, family size and age patterns, etc., reflecting a multiplicity of both ecological and cultural components. At the same time they are flexible, dynamic, and changing, depending on the needs of the family (Gonzalez 1985). In a home garden located in the Atlantic lowlands of Costa Rica, near the town of Puerto Viejo, Sarapiquí, mapping revealed considerable diversity and complexity within an area of approximately 3250 square meters (field problem report of Flietner et al., *in* Jaffe and Gliessman 1986). There were 26 species of trees, 16 perennial ornamentals, 8 annual/biennial crops and 6 herbaceous species in the garden at the time of the study (Table 4). The plants were distributed in what could be characterized as five functional areas, each area in a sense a separate agroecosystem, but overlapping and grading one into the other:

1. Low diversity, regularly patterned planting of crops of potential cash value, including tuber crops, pineapple, and young coconuts.
2. High diversity, irregularly patterned planting of trees, shrubs, herbs, and vines of many uses designed to satisfy domestic needs.
3. Low diversity, widely spaced planting of trees, most often with low

TABLE 4. LIST OF PLANT SPECIES ENCOUNTERED IN A HOME GARDEN AT LA GUARIA, PUERTO VIEJO DE SARAPIQUI, COSTA RICA, WITH THEIR USES

TREES		
Avocado	*Persea americana*	Fruit
Breadfruit	*Artocarpus altilis*	Fruit
Carambola	*Averrhoa carambola*	Fruit
Cashew	*Anacardium occidentale*	Nut
Cedro amargo	*Cedrela odorata*	Wood
Coconut	*Cocos nucifera*	Fruit, Wood
Giblon	*Spondias cytherea*	Fruit
Gitel	*Yucca gloriosa*	Flowers
Guanabana	*Annona muricata*	Fruit
Guava	*Psidium guajava*	Fruit
Laurel	*Cordia alliodora*	Wood
Lime	*Citrus limon*	Fruit
Mamon chino	*Nephelium lappaceum*	Fruit
Mamon verde	*Melicoccus bijugatus*	Fruit
Mandarin	*Citrus reticulata*	Fruit
Manzana de agua	*Syzygium jambos*	Fruit
Nance	*Byrsonima crassifolia*	Fruit
Naranjillo	*Solanum quitoense*	Fruit
Olive	*Olea europaea*	Oil
Papaya	*Carica papaya*	Fruit
Pejibaye	*Bactris gasipaes*	Fruit
Plantain	*Musa paradisiaca*	Fruit
Sour orange	*Citrus sinensis*	Fruit
Terminalia	*Terminalia catappa*	Wood
OTHER CROP PLANTS		
Azul	*Justicia tinctoria*	Dye
Cardamon	*Elettaria cardamomum*	Herb
Chayote	*Sechium edule*	Vegetable
Chile	*Capsicum annuum*	Vegetable
Malanga	*Xanthosoma sagittifolium*	Root
Malva	Unknown	Medical
Matalumbresa	Unknown	Medical
Oregano	*Lippia graveolens*	Herb
Ginger	*Zingiber officinale*	Herb
Pineapple	*Ananas comosus*	Fruit
Taro	*Colocasia esculenta*	Root
Yam	*Dioscorea* sp.	Root
Yuca	*Manihot esculenta*	Root
Sugar cane	*Saccharum officinarum*	Sugar
ORNAMENTAL PLANTS		
Pavonocillo	*Aphelandra* sp.	Ornamental
Bougainvillea	*Bougainvillea* sp.	Ornamental
Canna lily	*Canna generalis*	Ornamental
Gold dust croton	*Codiaeum variegatum* var. *pictum*	Ornamental
Prayer plant	*Calathea* sp.	Ornamental
Dahlia	*Dahlia excelsa*	Ornamental
Dumb cane	*Dieffenbachia* sp.	Ornamental
Caña de India	*Cordyline terminalis*	Ornamental
Rubber tree	*Ficus elastica*	Ornamental
Gardenia	*Gardenia* sp.	Ornamental
Hibiscus	*Hibiscus rosa-sinensis*	Ornamental
Hollyhock	*Althaea rosea*	Ornamental
Tea rose	*Rosa* sp.	Ornamental
Variegated philodendron	*Philodendron* sp.	Ornamental
Variegated cassava	*Manihot esculenta*	Ornamental
Zinnia	*Zinnia elegans*	Ornamental

grass or bare soil below, often used for social or recreational purposes.
4. Very high diversity, intercropped planting of ornamental herbs and shrubs planted very close to the house and cared for by the women in the household.
5. Moderate diversity, alternately planted fencerow surrounding the property primarily composed of fruit and firewood tree species.

The garden reflects an interaction between the need for domestic food or use items, the desire or need for cash income, personal preference and enjoyment, and the constraints of time and space. A move into cash cropping, relatively new to this particular garden, is changing its structure dramatically. This trend will continue as trees mature, markets change and the socioeconomic status of the family changes. Home gardens seem to incorporate this flexibility and dynamism.

AN EXPERIMENTAL AGROECOSYSTEM

The indigenous practices and management strategies observed on local farms can provide information useful for the design of resource-conserving, ecologically sound farming systems for the tropics. But this information needs to be tested, refined, and modified according to each farm and each farmer. Sites are necessary where such testing can take place. One such site occurs in Coto Brus, the southernmost county of Costa Rica.

A region that only 30 years ago was covered by rainforest, Coto Brus is currently predominantly devoted to the cultivation of coffee, secondarily to livestock, and otherwise used for annual crop production on a smaller scale. Growth in the region has been recent and rapid. Two sites stand out as valuable resources for carrying out agroecological research. The first, the OTS field station at the Las Cruces Botanical Gardens, has made it possible for naturalists and horticulturalists to study tropical biology, ecology, and horticulture in the field. The impressive plantings of plant species of horticultural value, native to Costa Rica as well as those brought from other parts of the tropical world, are an invaluable resource.

The other site is Finca Loma Linda, Costa Rica, a farm near the Panamanian border at Cañas Gordas. The owners, who homesteaded the farm in 1954, have been in Coto Brus during almost the entire settlement period. Their farm has gone through many changes and reorientations during that time. It currently employs a farm management strategy that lends itself exceptionally well to agroecological research. A significant portion of the 50-ha farm still has its original forest cover. This offers opportunities for simultaneous baseline studies. The rest of the land has been cleared for farming. The deep, porous, volcanic soils are excellent for agricultural use, but the hilly, sloping land is subject to erosion and loss. To solve this problem

and to facilitate a degree of mechanization on the farm, bench terraces were constructed (Fig. 4). The borders were planted to a vigorous clump-forming grass known locally as imperial grass (*Axonopus scoparius*). Since this grass grows quickly, it is cut frequently and the cuttings are used to mulch the soil, keeping the surface protected continuously and providing a valuable source of organic matter. This is important in an area with 3500-4000 mm of rainfall annually.

The terraces at Loma Linda have permitted the development of an intricate crop rotation scheme, detailed records of which go back almost 14 years. The scheme has included fresh market vegetables, basic grain crops, cut grass for animal feed, and even coffee. Generally speaking, the terraces have been managed during this time in ecologically sound ways, designed to reduce the need for outside input to a minimum, build soil fertility over time, hold pest problems to a minimum, and contribute to the sustainability of the productive capacity of the already cleared land. An agroecosystem designed and managed with these concerns in mind is an ideal location for an agroecological approach to researching the sustainability of agriculture in the tropics.

As an example of how to use such an experimental agroecosystem, research was carried out at Loma Linda during the OTS tropical agroecology course of August 1985. Experiments were carried out on such diverse topics as the impact of structural and species diversity of a crop on herbivore abundance, the effects of different species of plant mulches on bean growth, light capture by the foliage in monocultures as compared to polycultures, and populations as affected by the cropping pattern, distribution of mycorrhizae in the soil as impacted by cropping patterns, weed growth as impacted by monocultures as compared to polycultures, and allelopathic potential of different weeds on the terraces. These projects address important agroecological questions. The results are providing important baseline ideas for future research (Jaffe and Gliessman 1986).

The results of one project serve to illustrate the type of research that can be carried out in such a system. In this case, weed biomass was determined and compared in mature monocultures of corn, beans and squash and in the polyculture of all three (Bergmark et al. *in* Jaffe and Gliessman 1986). Plots were set up at Finca Loma Linda to test the hypothesis that the vegetative canopy of a polyculture system has a more complex structural diversity, hence an enhanced ability to capture incoming solar radiation. It was hypothesized that the increased shading possible in the polyculture should lead to a reduction in weed biomass. The plots were planted in May, followed by a uniform weeding six weeks later, with the final sampling of above-ground live biomass of the weeds taken five weeks after that.

As can be seen in Table 5, there are trends in weed weight distribution

according to the crop type, although variability in sample weights led to a lack of statistical significance between treatments. At the time of the sampling, the squash monoculture cover had only partially covered the plots, bean cover was fairly limited, and densest cover was observed in the corn monoculture and the polyculture. Total weed biomass under the corn and squash systems were the same. Biomass from the bean plots was 23% greater and weed biomass from the polyculture system was approximately 10% less than the corn or squash systems. Monocots accounted for a lower proportion of the bean plot weed weight (about 10% of the total biomass) than the corn (27% monocots), squash, or polyculture (34 and 35% monocots). However, actual mean weights of the monocot biomass varied little between treatments. The percent light transmission (calculated as the percent of transmitted light reaching the soil surface in each crop system as compared to that reaching an unplanted soil surface adjacent to the plots) again showed similar trends, but variability in this sampling again ruled out statistical significance. The highest light transmission was recorded in the bean monoculture, correlating to the lower cover produced by the bean crop. The lowest transmission occurred in the corn monoculture. The trend for lower weed biomass in polyculture, then, is only partially related to light reception by the crop canopy. Since many factors come into play in such an interactive system, detailed, long-term research is necessary to determine their relative importance (Gliessman 1986).

PERSPECTIVE FOR THE FUTURE

An agroecological focus on tropical agriculture goes beyond crop yields. It delves into the complex set of factors that make up the agroecosystem. Local, indigenous agroecosystems that have evolved under the diverse and often limiting conditions of the tropical environment are adapted to this set of factors. The agroecosystems have evolved through time as reduced external-input systems, with a greater reliance on renewable resources and an

Fig. 4. (Adjacent page). A diversified terrace agroecosystem at Finca Loma Linda, near Cañas Gordas, Coto Brus, Costa Rica. Each terrace is separated by a border planted to imperial grass (*Axonopus scoparius*) to be cut periodically and used as a protective mulch. Plantings from right to left are butter lettuce, curly leaf lettuce, radishes, and an experimental planting of corn/bean/squash monoculture and polycultures. Undisturbed rainforest can be seen in the background. Photo by S. Gliessman.

TABLE 5. MEAN FRESH WEIGHT (GM/0.2 M SQ) OF THE ABOVEGROUND WEED BIOMASS IN CORN, BEAN, AND SQUASH MONOCULTURES COMPARED TO A POLYCULTURE OF ALL THREE[a]

Crop System	Mean Fresh Weight of Weeds Total	Monocots	% Light Transmission
Corn monoculture	61.8	16.8	36.06 ± 03.8
Squash monoculture	61.4	20.8	51.40 ± 31.2
Bean monoculture	79.8	14.9	74.50 ± 22.7
Polyculture	55.0	19.0	44.70 ± 25.5

[a] Percent light transmission was determined by measurements at the soil surface in each crop system with a LI-COR quantum radiometer and PAR sensors. Biomass figures are the means of three samples taken in each plot, and light figures are the means of 10 readings taken at 50-cm intervals in each plot.
From: Bergmark et al. *in* Jaffe and Gliessman 1986.

ecologically based management strategy. A research focus in agriculture that can take advantage of this knowledge and experience can permit us to explore the multiple bases upon which sustainability rests. It represents the blending of knowledge gained by ecologists studying the dynamics and stability of natural tropical ecosystems with the knowledge of farmers and agronomists on how to manage the complexities of food-producing agroecosystems. From this can come the sustainability in the production base so critical for the long-term cropping of cleared lands in the tropics. By keeping the farmer on his or her land and by ensuring the maintenance of that farm, pressures that are currently having drastic impacts on tropical rainforest reserves can be considerably reduced. Sustainability in the natural resource sector, therefore, becomes inseparably linked to sustainability in the agricultural sector. An interdisciplinary approach is vital to ensure success.

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ECOLOGY AND MANAGEMENT OF MIGRATORY FOOD FISHES OF THE AMAZON BASIN

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Geographically, the Amazon is defined by its drainage basin, and the aquatic environment is a good place to begin looking for possible far-reaching biological interactions that can be used as natural guidelines for management and conservation considerations. Fish, because they are undoubtedly the most abundant and diverse vertebrate group in Amazonian waters, are the most likely candidates for providing evidence of ecological interactions that embrace huge geographical areas of the immense river system. Furthermore, piscine communities represent most of the standing aquatic animal biomass (Bayley 1982).

The Amazon river system drains four principal geological regions embracing an area of about seven million km^2: the Andes, the Amazonian Lowlands, the Guiana Shield, and the Brazilian Shield (Fig. 1). Surface geology (soils) and relief (erosion factors) largely control the hydrochemistry of Amazonian waters (Gibbs 1967; Sioli 1968; Furch 1984). The most notable fact of the surface geology of Amazonia is its highly eroded and leached state, and consequently, nutrient-poor soils. The rivers and streams rising on the Guiana and Brazilian Shields, and in the Amazonian Lowlands, reflect the nutrient poverty of the soils of their drainage basins. Most of the Brazilian and Guiana Shield rivers have relatively clear waters because of the low suspended loads that they transport. In the Amazonian Lowlands, there are also a large number of blackwater rivers whose waters are stained by organic compounds derived from terra firma plant communities (Klinge and Ohle 1964; Leenheer and Santos 1980) (Fig. 2). Swampy floodplain areas also produce blackwater where there is an incomplete breakdown of organic matter. Clearwater and blackwater rivers, of which there are several chemical types, account for most of the primary, secondary, and tertiary tributaries of the Amazon river system.

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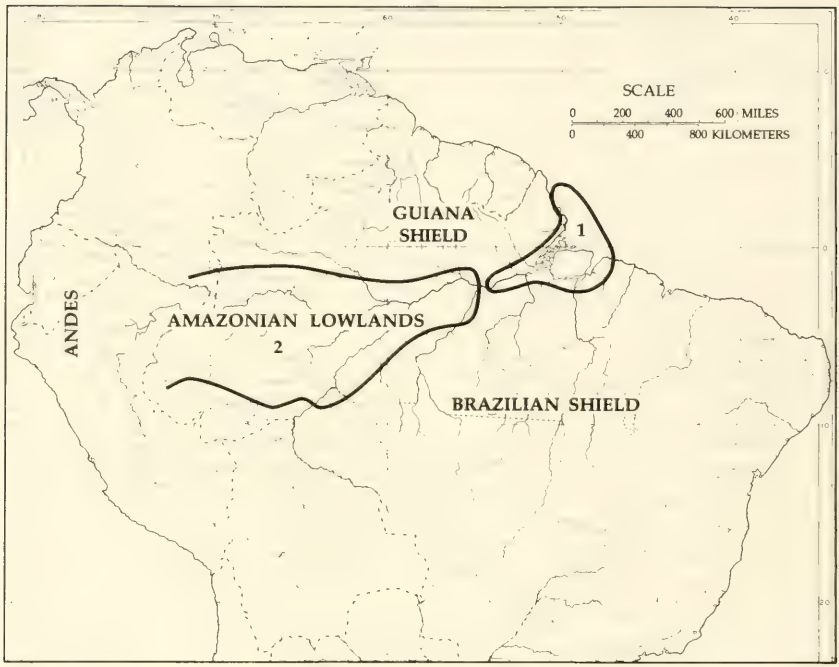

Fig. 1. The Amazon Basin drainage. Region 1 is the Lower Amazon and estuary; this area is an important nursery habitat for large predatory catfishes. Region 2 is the Central Amazonian Lowlands wherein migratory characin fishes have life histories that embrace several river types. The two regions are linked ecologically via the predatory catfishes that migrate upstream out of the estuarine area to feed on the migratory characins. See text for details.

Therefore, most Amazonian rivers and streams are relatively nutrient-poor, and *in situ* primary production is low (Furch 1984; Rai and Hill 1984).

The Amazon river system drains a 3000-km arc, extending from Bolivia to Colombia, of the eastern versant of the Andean mountain chain. In contrast to the Amazonian Lowlands and the Shield regions, the Andes combine high annual rainfall and recent uplift producing topographic relief, the latter with relatively rich soils. These factors result in the large suspended loads of the rivers that tap the Andes, and likewise, their higher nutrient levels compared to their blackwater and clearwater counterparts that are found farther to the east. The Andean affluents descend into the Amazonian Lowlands as turbid water rivers and are usually so muddy that transparency is reduced to a few centimeters. Due to the fact that several of the large tributaries that rise in

Fig. 2. Landsat satellite image of the area near the confluence of the Rio Solimões (Amazon River) and Rio Negro. The Rio Negro is a blackwater river, whereas the Rio Solimões is highly turbid because of the Andean sediments it transports. The numerous floodplain lakes and lagoons along the Rio Solimões are annually injected, during the floods, with Andean nutrients carried downstream by the main channel. The areas of highest aquatic primary production in the Central Amazon are found in the floodplain lakes of the turbid water rivers whose headwaters rise in the Andes. The Andean nutrients are sufficient to sustain relatively high phytoplankton and herbaceous plant production, at least during part of the year. The turbid river floodplains are used as nursery habitats for many of the migratory characin species that, as adults, disperse to the nutrient-poor blackwater and clearwater tributaries where they enter the extensive flooded forests to feed on fruits, seeds, detritus, insects, and many other food items that are available in this habitat. See text for details.

the Andes only merge with the main Amazon river 1000-2500 km downstream, there is a roughly triangular region between the high mountains and the mouth of the Rio Madeira (with apex there) that is traversed by six major turbid tributaries. The hydrochemical effects of the Andes–i.e. heavy sediment loads, high turbidity and relatively high nutrient levels–extend via the rivers across the western and central Amazonian Lowlands, greatly increasing the limnological diversity of the region.

The total suspended load ushered into the Amazon river from Andean affluents is sufficient to render the main trunk highly turbid all the way to the Atlantic. The large amounts of Andean alluvium, and associated dissolved nutrients in the water column, that are annually injected into Amazonian floodplains represent, in effect, a geological and nutrient extension of the high cordillera to the west.

The principal pathways of primary production in Amazonian rivers are floodplain/riparian forests, phytoplankton, and aquatic herbaceous plants. The relative importance of each is largely determined by hydrochemistry and morphological features of the river. Phytoplankton production in general is limited in Amazonian river channels either because of poor transparency or low nutrient levels. The single most important area of phytoplankton production, vis-á-vis fish production, appears to be the estuary, though this area has never been investigated in detail. The mixing of Amazon and oceanic waters leads to increased transparencies that, in combination with the accumulation of Andean nutrients, results in intensive and sustained algal blooms (Egler and Schwassmann 1962).

The highest phytoplankton production of inland Amazonia is found in floodplain waterbodies that are annually inundated with waters transporting Andean nutrients (Schmidt 1973a, 1973b; Rai and Hill 1984). These are associated with rivers such as the Amazon, Madeira, Purus, Juruá and a few others of smaller size. Leaving nutrient factors aside, total primary production of phytoplankton in Amazonian floodplains is limited mostly by the relatively small area that is occupied by open waterbodies (where light conditions are satisfactory) and to the seasonal shrinking of these lakes and lagoons during much of the year. None of the important commercial fish species whose life histories are restricted to the central Amazon have food chains that are linked to phytoplankton. Fisheries based on phytoplankton-derived food chains are found in the mouth lakes of some of the eastern clearwater rivers, such as the Xingu and Tapajós, but these offer very limited annual catches because of the nutrient-limited gross primary production of these waterbodies.

Aquatic herbaceous plants in the Amazon river system are most closely associated with river edges and floodplains that are laved annually by waters containing Andean nutrients. These herbaceous communities are often referred to as floating meadows because most of the biomass is buoyant with emergent

stem and leafy parts (Junk 1970). Floating meadows are productive communities, but their extent is limited by one or more of the following factors: currents (especially in river channels), depths greater than about 10 m (especially in floodplain lakes during the high-water period), low nutrient levels (especially in many clearwater and blackwater rivers), low-water periods that result in die-offs or dormancy and floodplain forests that shade out aquatic herbaceous plant production (Junk 1984). In waterbodies receiving Andean nutrients, primary production of herbaceous plants may exceed that of phytoplankton, though few comparative data are yet available to determine the relative scales (Bayley 1980; Junk 1984). In most clearwater and blackwater river systems, herbaceous plants play a very minor role in primary production. Floodplain forest die-offs in such systems, due to natural causes or dam building, can lead to large-scale tree decomposition, and consequently to the establishment of a nutrient base for the development of floating meadows.

The floodplains of the Amazon Lowlands are covered mostly with rainforest that is subject to annual inundations of two to ten months each year, depending on the intensity of the floods and the local topography (Fig. 3). The total flooded forest area of Amazonia has not yet been measured with accuracy, but it appears to cover an area of at least 100,000 km^2. Amazonian flooded forest is not homogeneous in physiognomy, floristics, or temporal patterns of inundation, and several plant formations are recognized (Prance 1978; Goulding 1980). The most abundant is *seasonally flooded forest* that is inundated during most years. In the central part of the Amazon Basin, floodplain forest is inundated for about six months annually. In the lower Amazon river, below about the Rio Xingu, there is a large labyrinthine delta consisting of many low-lying islands that are subject to flooding twice daily because of the influence of the oceanic tides. These islands, with the major exception of the eastern half of Marajó, are covered mostly with rainforest. *Tidal flooded forest* area may exceed 20,000 km^2 and most of it is inundated for 8-12 hours each day.

FAR-REACHING FISH LIFE HISTORY PATTERNS IN THE CENTRAL AMAZON

The Central Amazon has thirty or more fish species whose life histories involve the use of various river systems and habitats. These species get from one river or habitat to another by making migrations, and these movements are usually seasonal and heavily exploited by commercial fishermen (Goulding 1983; Smith 1981; Ribeiro 1983). To illustrate the way in which many Central Amazon fish species use various river types and habitats, the life history of an important commercial species, *Colossoma macropomum* (Characidae), will be discussed.

Fig. 3. Flooded forest of the Rio Negro. Only the canopy is above water. Water depth at this particular spot was about 12 m. The tree on the far right is *Hevea guianensis*, a species whose seeds are eaten by many Rio Negro fish taxa.

Colossoma macropomum is the largest characin (a group to which belong the tetras, cardinals, and silverdollars) in the Amazon (Figs. 4, 5). It reaches lengths greater than one meter and weights in excess of 30 kilograms. In the late 1970s, this species alone accounted for over 40% of the total commercial catch sold in Manaus, the largest fish market of inland Amazonia (Petrere 1978).

The life history of *C. macropomum* in the Central Amazon involves the use of all the major river types of the region. The young of the species are largely confined to the floodplains of the turbid water rivers receiving Andean nutrients; fisheries data suggest that the Rio Solimões-Amazonas and Rio Purus are the most productive of *C. macropomum*. Detailed studies of the diet of young *C. macropomum* reveal that these age classes feed mostly on zooplankton and fruits and seeds (Carvalho 1981; Goulding and Carvalho 1982). Only rivers receiving Andean nutrients in extensive floodplains are productive enough of zooplankton to support large populations of young *C. macropomum*. Zooplankton appears to remain important in the diet of the species until it reaches maturity at about 55 cm in length, or approximately 4-6 kg in weight. Fruits and seeds are also eaten in large quantities by young *C. macropomum*, and especially during the high-water period when these items are abundant in the flooded forests. Numerous, fine gillrakers and molariform-like teeth allow the young fish to eat two disparate types of foods that, alone or in combination, are relatively abundant throughout the year.

At about 55 cm length, and perhaps 4-5 years of age, *C. macropomum* begin to migrate out of the floodplains to the river channels. It is still unclear whether the fish are fully mature when they first migrate, but nevertheless they begin to display the behavior of adults. At the beginning of the annual floods, large schools of adult and fully ripe *C. macropomum* are encountered moving upstream in the turbid water rivers of the Central Amazon. When water level begins to rise rapidly, the species spawns in the river channel. It appears that both fertilized eggs and newborn are carried downstream for several days before the fry find their way into the adjacent floodplain waterbodies that serve as their nursery habitats (Lima 1984 and pers. observ.). The upstream movement of the adults in the turbid water rivers during the prespawning period is hypothesized to counterbalance the downstream displacement of fry before they have a chance to enter floodplain nursery habitats (Goulding and Carvalho 1982).

After spawning, which coincides with rapidly rising water levels, the spent fish migrate to floodplain forests, which at this time are rapidly being inundated. Adult *C. macropomum* appear to prefer forests flooded by blackwaters or clearwaters (which can also be some of the floodplain areas of the turbid water rivers). This functionally displaces the largest part of the adult biomass away from the nursery habitats where the young are found.

Fig. 4. The tamaqui (*Colossoma macropomum*, Characidae), the most important food fish species in the Central Amazon in the 1960s and 70s. The species is being overexploited by commercial operations.

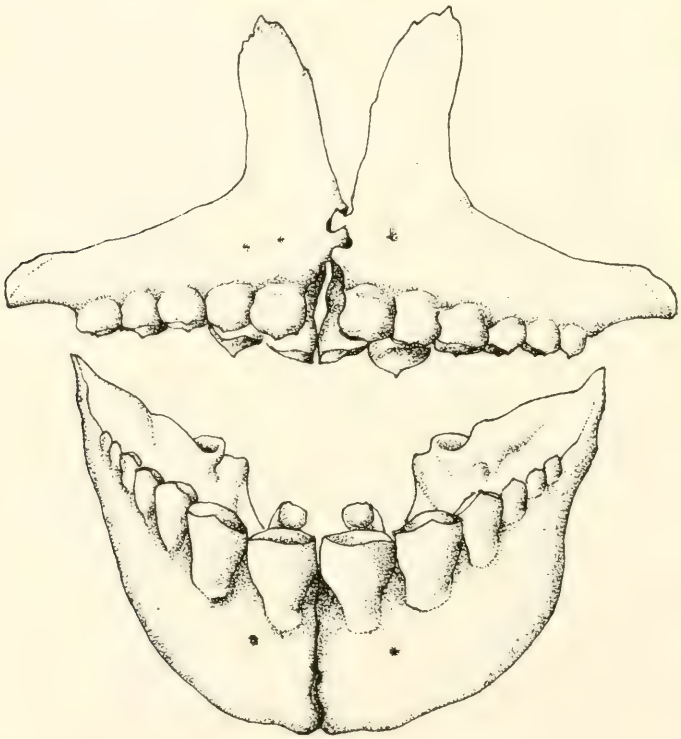

Fig. 5. The molariform-like dentition of *Colossoma macropomum*. With this type of dentition, the characin is able to crack hard nuts.

Adult *Colossoma macropomum* feed mostly in flooded forests where they take a large number of items, though fruits and seeds are by far their most important foods. Because of its robust size and extremely strong molariform-like dentition, *C. macropomum* is able to masticate large and often hard nuts that most other fish species are unable to crush, swallow, or digest. For example, rubber trees (*Hevea* spp.) produce large dehiscent capsules that, when ripe, explode and eject two or three seeds. The seeds of *Hevea spruceana*, one of the favorite foods of *C. macropomum*, are 3-4 cm in length and have a hard nut wall. The large characin easily crushes rubber tree seeds, and a 10-kg fish feeding in flooded forest will often have over one kg of this item in its stomach and intestines, that is, over 10% of its own body weight. The fish can even crack seeds harder than Brazil-nuts as, for example, those of a common floodplain palm (*Astrocaryum jauari*). The species also eats quantities of fruits that are invested with fleshy pulps or arils. In many cases the seeds of these fleshy fruits are not masticated, and they are probably dispersed when defecated.

During the flooding season, *C. macropomum* lays down large fat stores in its body cavity and tissue. These energy reserves often exceed 10% of its total body weight (Castelo, Amaya, and Strong 1980). At the end of the annual floods, when river levels fall rapidly, the fishes are forced out of the floodplain forests. The adults migrate down the blackwater or clearwater tributaries and occupy the turbid river channels. Adult populations also move out of adjacent floodplains of the turbid water rivers. The river channels offer little food for *C. macropomum* during the low-water period. This species, and others like it such as *Piaractus brachypomus*, apparently live mostly off their fat reserves until the subsequent annual floods when they return to flooded forest following breeding.

In sum, the life history of *C. macropomum*—and other species with a similar ecology—involves the use of the limited areas of high primary production that sustain dense zooplankton concentrations and, to the other extreme, the far-flung flooded forests, inundated by nutrient-poor waters, which nevertheless receive a large input of fruits, seeds, and other organic matter on which many fish species depend. The total area occupied by fishes whose life histories embrace the flooded forests of the far-flung blackwater and clearwater tributaries and the turbid river channels and their adjacent floodplains probably exceeds 2 million km^2 (see Fig. 1 for the approximate area occupied by the migratory pattern outlined above). It is still not known whether the migratory characin species of the Central Amazon are each represented by single populations over the enormous area, or whether several distinct populations are involved. The author suspects that only one population is involved in most cases, as migratory schools are seen, and captured by commercial fishermen, when moving from one tributary system to the next.

THE MIGRATORY LINK BETWEEN THE CENTRAL AMAZON AND THE ESTUARY

The Amazon Basin has over a dozen species of predatory catfishes of the family Pimelodidae that reach over 50 cm in length (Goulding 1981). The dourada (*Brachyplastystoma flavicans*) and piramutaba (*Brachyplatystoma vaillantii*) are the most important commercial species. *Brachyplastystoma flavicans* is captured in large quantities in both inland waters and in the estuary, whereas *B. vaillantii* is exploited mostly near the Rio Amazonas delta region, though it is found over a wide area of the Amazon Basin. This discussion will focus on *B. flavicans* because it is the species that has been most studied, and it serves to illustrate a main ecological link between the estuary and the Central Amazon (Fig. 6).

Brachyplatystoma flavicans is found in all of the major river types of the Amazon. The species, in the Central Amazon, is confined mostly to river channel habitats; it is seldom captured in floodplain waterbodies. Experimental fishing and length measurements of over 10,000 specimens captured in the Madeira, Solimões-Amazonas, Purus and Juruá rivers revealed that individuals of less than about 50 cm are rare in the Central Amazon, and the small size classes are only abundant in the Lower Amazon, that is, below about the mouth of the Rio Tapajós. The average-size *B. flavicans* captured in the Central Amazon ranged 81-94 cm in length. In striking contrast, the average-size *B. flavicans* of the Belém market, supplied mostly from estuarine catches, was less than 60 cm; furthermore, in and near the estuary, a full range of size classes have been observed, which was never the case in the Central Amazon. Larval *B. flavicans* have also been captured in the estuary (Barthem 1985), and this evidence, along with that cited above, strongly indicates that the species spawns somewhere in the lower Rio Amazonas or near its confluence with the Atlantic Ocean (and perhaps northwards along the Amapá coast, since the freshwaters of the Rio Amazonas are deflected northwards by oceanic currents).

Although larvae have been located, neither fishermen nor our experimental fishing efforts have revealed the whereabouts of mature, breeding populations. The few unquestionably mature females that have been captured were all over 120 cm in length, and only rarely do individuals of this size appear in commercial catches.

The evidence available suggests that there is a striking separation of the small and medium size classes of *B. flavicans*. The younger fish appear to be confined mostly to the Lower Rio Amazonas and its estuary, whereas the large size classes move upstream (after about 60 cm length?). Upstream migrations are easily observed, and they are annually exploited by commercial fishermen. These upstream migrations involve not only the Rio Solimões-

Fig. 6. A catch of the *Brachyplatystoma flavicans* in the upper Rio Madeira region. The catfish appears to breed in the estuary, which is also the nursery region for the species. The estuary offers high primary production to sustain a large biomass of young predatory fishes. Pre-adults migrate upstream and out of the estuary and to Central Amazonian waters where they feed on migratory characins and other fishes. The fishes shown in the photograph were over 2000 km from the estuary, from where they are thought to have been recruited. See text for details.

Amazonas, but also many if not most of its tributaries. The catfish migrations have been investigated in some detail at the Teotonio rapids, some 900 km up the Rio Madeira, and nearly 2000 km from the estuary (Goulding 1979, 1981). The fishes are easily seen at the rapids and thus their seasonal upstream movements can be monitored. It appears logical to hypothesize that, at some point in their life history, the upstream migrating *B. flavicans* schools return downstream to breed in the estuary. These hypothesized downstream migrations, however, have not been observed, probably because they take place during high water and in the middle of the river channel. Swift currents, deeper water, and much plant debris make for difficult fishing in the river channels during the floods, and thus commercial operations do not indicate the presence of downstream-moving fishes.

Over 5000 specimens of *B. flavicans* captured in the central Amazon

were examined for prey contents, and the feeding behavior of upstream migrating schools was also observed. These data reveal that they feed mostly on prey that is 15-25% of their own length. The medium-size migratory characins were the most common prey fishes consumed. The large predatory catfishes often follow and feed on the migrating characins. This feeding activity appears to continue for about six months each year. During the floods, the characins, and most other prey, spawn and then migrate to the flooded forests where they feed. As mentioned above, *Brachyplatystoma flavicans* are rarely found in flooded forests, and thus, for reasons that are not clear, do not follow their prey into this habitat. Our evidence suggests that the floods represent a period of reduced feeding for the predatory catfishes because prey is rare in the channels at this time of year. This is the opposite of the case of the migratory characins, whose main feeding period is during the floods when they move into flooded forests (Goulding 1980).

If the predatory catfishes spawned in the inland waters of the Central Amazon, then almost undoubtedly their large biomass of young fish could only be nourished in floodplain waterbodies, because only therein would primary production be great enough to support a foodchain sustaining them. As it is now, these floodplain habitats have a relatively large number of other predatory taxa, such as cichlids (*Cichla* spp.), piranhas, *Hoplias* spp., and the largest fish of the Amazon, the pirarucu (*Arapima gigas*). By using the estuary as a nursery habitat, the large catfishes are able to tap habitats of high primary production, that is, via the shrimp, small fishes, and other primary and secondary consumers that they eat (Barthem 1985). The characins are apparently much less tolerant of brackish water than are some of the large predatory catfishes, and few of the former are found in the estuarine waters. After reaching about 60 cm in length, the catfishes begin to leave the estuary and migrate upstream, at which time they become linked to a foodchain based mostly on floodplain primary production (see Figure 1 for the two principal trophic regions of *B. flavicans* in the Amazon system). The floodplain energy is transferred from the flooded forests, herbaceous plants, and phytoplankton as prey in the form of migratory characins and other fishes.

MANAGEMENT OF MIGRATORY FOOD FISHES

Biologists and management authorities concerned with the Amazon Basin fish fauna have in general taken a relatively reductionistic approach toward its understanding. The trend has been to study small areas or a few species-restricted habitats and then extrapolate from the data gathered for the Amazon Basin as a whole. At present few data on the commercial fisheries are being gathered by government authorities, despite the fact that total

catches delivered to the major markets appear to be decreasing. Catch estimates are based on data collected in the 1975-1980 period, but my own observations suggest that effort and yield patterns have changed considerably since then (Petrere 1978; Goulding 1979, 1981; Smith 1981).

Bayley (1981) and Bayley and Petrere (1986) attempted to estimate total fish yield, including commercial and subsistence fisheries, for various parts of the Amazon Basin; the authors suggest a 198,000 t/yr total yield for the Amazon Basin as a whole, but I believe this estimate could be short or long by perhaps a 100,000 t/yr because of the relatively restricted data bases from which it was extrapolated. Unless market and subsistence data are collected, a better estimate will not be possible.

Amazon commercial fisheries are still largely based on the migratory species. Bayley (1981) and Bayley and Petrere (1986) imply that it would be too expensive from a management point of view to maintain high yields of the migratory species of large size such as *Colossoma macropomum* and *Brachyplatystoma* spp. There is some evidence that suggests just the opposite. For example, *C. macropomum* fish culture research has advanced considerably in recent years, and the species is now being artificially spawned in captivity (Woynarovich 1986). Amazon floodplain lakes could be restocked relatively cheaply with young *C. macropomum* on an annual basis, and this would help circumvent any recruitment failure that results from either over-fishing adults or from other causes. The *Brachyplatystoma* catfishes are only being overexploited because of industrial-size export fisheries operating in the estuary. The prohibition of export fisheries is a step much needed for Amazon fish resource management, and it would not be expensive to implement.

The management of Amazonian fisheries would be much easier if the important commercial taxa were not migratory and did not have life histories that include diverse river types and habitats that cover huge drainage areas. The migratory fishes and the fisheries for them should not be *written off* by scientists and management authorities because they appear to be more difficult to understand than a non-migratory situation. I suspect that the maintenance of the migratory fishes will be necessary if the relatively high yields now enjoyed are to continue. This suggests that research and management programs need to develop models that cover both large parts of the Amazon Basin and the extensive fish migratory network that exists in this system, and on which the most important commercial fisheries are based.

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ETHNOBOTANY AND CONSERVATION IN THE GUIANAS: THE INDIANS OF SOUTHERN SURINAME

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> *There is still a vast amount of field work to be undertaken, not only [in Guyana], but in Suriname and [French Guiana], and if haste be not made, the information which it is now possible to glean will probably be lost forever. The so-called opening up of the country for the trader, the rancher, the timber-getter, the balata and the rubber bleeder . . . may or may not exert a beneficial influence on the welfare of the Creole, the Negro, and the European, but for the aboriginal Indian it means ruin, degradation and disappearance.*
>
> *W. E. Roth, 1916*

Tropical forests are being destroyed, and many species are being lost. Although the problem is not widely recognized, the knowledge of how these species might prove useful for human welfare is disappearing even faster than the species themselves as tropical forest peoples relinquish their traditional lifestyles. This paper gives an overview of the situation in southern Suriname. Climate, vegetation, botanical, and ethnobotanical history are reviewed and the situation of the three local tribes (Tirió, Wayana, and Akuriyo) is discussed.

The tropical forests of the world are being destroyed at an alarming rate. As these forests are cut down, countless species of both plants and animals face certain extinction. At the same time, we are witnessing the disappearance of tropical forest peoples through acculturation and/or outright tribal extinction. These people have a profound knowledge of these forests and the useful products they contain. Failure to document this information would represent a serious economic and scientific loss for mankind.

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Ethnobotany—the study of tribal peoples' utilization of forest plants—has been the key to discovering species that are of major importance in both industrialized and developing worlds. Typical breakfast foods such as cornflakes, citrus juice, coffee, tea, hot chocolate, and hashbrown potatoes are based on forest plants that were first "discovered" and cultivated by tropical peoples. Nevertheless, *most* ethnobotanical information remains undocumented, and even in some of the least deforested tropical countries—such as Suriname—the knowledge of the utility of local flora is being lost.

SURINAME

The region known as Guiana is that area of land in northeastern South America bounded by the Río Orinoco, the Casiquiare Canal, the Río Negro and the Amazon. Since this region is surrounded by water, it was once common to refer to it as the "Island of Guiana" (Harris 1928). Today, Guiana has been divided into parts of Venezuela and Brazil, and into the countries of French Guiana, Guyana (formerly British Guiana) and Suriname (formerly Dutch Guiana). The term "the Guianas" refers to these small countries on the northeastern Atlantic coast of South America (Fig. 1).

There is some doubt as to the origin of the term "Guiana." In several Carib languages, the suffix "-yana" means "people" or "tribe" (e.g. "Okomoyana" = "wasp people," "Tunuyana" = "water people"). I contend that the term "Guiana" originated as a corruption of "Wayana," the name of an Indian tribe in the interior. This region was discovered by the Spaniards, and cartographers working with the explorers filled in the interiors of these regions with the names of both topographical features and local tribes. The letter W is not common in Spanish; thus, a Spanish cartographer hearing of the Wayana tribe might write "juyana" or "juayana" on his map. An Englishman reading the "j" as a "g" would pronounce it "Guiana" or "Guyana."

Due to their colonial heritage, the Guianas are seldom associated with the Iberian influence so predominant in the rest of South America. Nevertheless, the first explorers were Spaniards, Ojeda and de la Cosa. It was not until the end of the sixteenth century that Sir Walter Raleigh landed in the Guianas, and he was then followed by the Dutch and the French (Harris 1928).

Bordered by Guiana to the west, French Guiana to the east, and Brazil to the south, Suriname (formerly spelled "Surinam") was first settled as a colony when Lord Willoughby established sugar plantations along the Suriname River in 1650. The colony was then taken over by the Dutch in 1667 in exchange for Nieuw Amsterdam (New York) as part of the settlement of the Second Anglo-Dutch War. As a result of wars and shifting political alliances in Europe, control of Suriname changed back and forth between England and Holland during the nineteenth century and then became a full-fledged Dutch

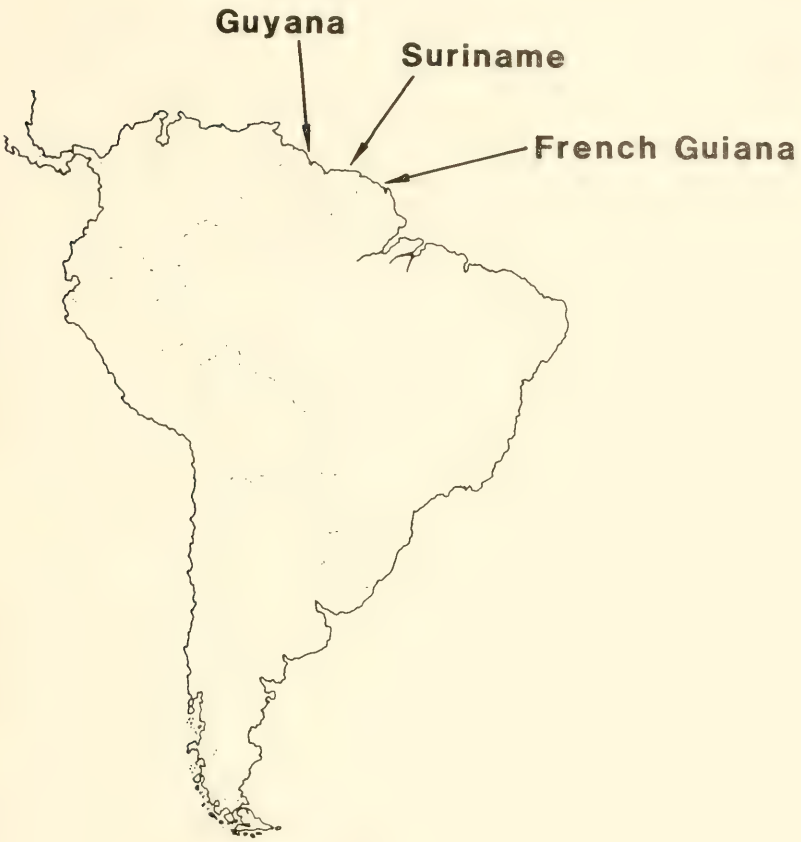

Fig. 1. The Guianas.

colony in 1833 (Sanderson 1939). The Republic of Suriname became independent from the Netherlands on November 25, 1977.

Suriname has a population of about 377,000, making it one of the least populated countries in South America, with a population density of only 2.3 people per square kilometer. The country is noteworthy for its extraordinary ethnic composition. Sanderson (1939) wrote: "A tourist with five weeks at his disposal can visit Suriname and see the real virgin jungle, aboriginal Amerindian settlements, African tribal life, [Indonesian] dances and festivals, Hindu temples, queer animals [and] Dutch canals."

Like many of the Caribbean countries, the largest segment of the population is composed of blacks who are, for the most part, descendants of African slaves. The black population consists of two groups: the city blacks, known as "Creoles" and the Bushnegroes. As in neighboring Guyana, the urban blacks

are the most politically powerful ethnic group in the country. There are also sizeable populations of Hindustanis, Javanese and Chinese who are descendants of contract laborers who migrated to Suriname when slavery was abolished in 1863. There is also a European element, comprised mostly of people of Dutch and Middle Eastern ancestry (Sanderson 1939). Although the official language is Dutch, the *lingua franca* is Sranan (also known as Nengre and Taki-taki); it is essentially a mixture of Dutch, English, Portuguese, and French, with some African, Amerindian, and Hebrew words.

CLIMATE

Suriname has a tropical climate with prevailing trade winds from the northeast. The mean annual daily temperature is 26.1°C with little monthly variation (Lindeman and Moolenaar 1959). The warmest months are September and October and the coolest is February (Rivière 1969). The relative humidity is consistently high, averaging 80% near the coast to as much as 95% in the rainforest (Lindeman and Moolenaar 1959; Schulz 1960).

Suriname has four seasons, unequal in length: the "big" wet season (April to July); the "big" dry season (August to November-December); the "little" rainy season (December to January-February), and the "little" dry season (February to March-April); (Lindeman and Moolenaar 1959; Kloos 1971). May and June are the wettest months, while September and October tend to be the driest (Rivière 1969).

Although Suriname is sometimes considered to be part of the Caribbean in a cultural sense, it lies outside the path of Caribbean hurricanes. Coastal winds can be very strong; however, the rainforests of the interior are little affected by the hurricanes and typhoons, which, in contrast, do influence successional stages of the tropical forest in the Far East (Whitmore 1975).

GEOLOGICAL SETTING AND VEGETATION

Geologically, Suriname can be divided into two major regions: the coast and the interior (O'Herne 1966; *in* Mittermeier 1977). The coast can be subdivided into the young and the old coastal plain. The young coastal plain is comprised of fluvio-marine deposits of fertile heavy clays and is covered with mangrove forest, herbaceous swamp, and swamp forest. To the south of this subregion lies the old coastal plain, which is made up of nutrient-poor, white sand or dusty clay-bearing swamp forest in the low-lying areas and marsh forest or high forest on the ridges (Vink 1977).

The interior region can be subdivided into the savanna belt to the north and the rainforests of the interior. The savanna belt consists of infertile coarse, bleached or unbleached sands or sandy clays, with good drainage; it

supports a savanna vegetation. Only 7% of the savanna belt is open savanna; the remainder is covered with savanna forest (Vink 1977).

Larger than the other three regions combined, the rainforest belt lies on the northern section of the Guiana shield. This geological formation is Pre-Cambrian in age and is comprised mainly of granites and granito-schists, with a number of intrusions by long dolomite dikes (Lindeman and Moolenaar, 1959). The terrain is undulating and covered with tropical rainforest. In the center of this region stands the Tafelberg, a large block of Roraima sandstone that has resisted erosion and reaches a height of 1026 meters. The Tafelberg harbors a unique flora, very distinct from that of the surrounding rainforests.

Suriname lies in the central part of the Guiana region and lacks any phytogeographical division in terms of major mountain chains within its borders. Consequently, Suriname is contained completely within the distribution of most species present (Lindeman and Moolenaar 1959). Once the vegetation has been studied in greater detail, it may prove possible to subdivide some of the rainforest into types like the "Wallaba" forest (as described by Richards [1952]), based on a particular species (or number of species) that predominate. Until these studies have been conducted, the rainforests of southern Suriname may be classified according to the system proposed by Beard (1944) as seasonal evergreen forest or as in the systems proposed by Richards (1952) and Lindeman and Moolenaar (1959). The Acarai and Tumac-Humac mountains (740 m) form the border between Suriname and Brazil. With the exception of the Sipaliwini savannas, an extension of the Brazilian Paru savannas that reaches into southernmost Suriname, these border mountains are covered with tropical rainforest and are the source of most of the major rivers of Suriname. These rivers flow north through numerous rapids and waterfalls (which kept the Indians of the interior quite isolated until relatively recently) as they descend to sea level and empty into the Atlantic Ocean.

BOTANICAL HISTORY

The first major publication on the vegetation of the Guianas was Aublet's *Histoire des Plantes de la Guiane Françoise* (1775). Aublet's work was based on personal collections made between the years 1762-1764, which were probably supplemented with material collected by Amerindians and other locals (P. Grenand, pers. comm.). Aublet described many species and over 200 genera new to science, including the economically important genus *Hevea*. Howard (1983) pointed out the difficulties in updating some of Aublet's names due both to disagreements between text and illustration and to descriptions based on mixed collections. While Howard focused on species

described by Aublet, Zarucchi (1984) reexamined the generic names and clarified their current status. These two papers have cleared up much nomenclatural confusion regarding taxonomy of the plants of the Guianas.

Although many of the species described by Aublet occur also in Suriname, the first major publication to consider the plants of Suriname was Linnaeus' *Plantae Surinamenses* (1775), based on collections by Allamand and Rolander. Seventy-five years later, Miquel (1850) published *Stirpes Surinamensis Selectae*, which he based on plants collected by Focke (1835-1850), Keye (1844-1845), Splitgerber (1837-1838) and Weigelt (1828).

A major figure in the history of the botany of Suriname was A. A. Pulle, who published *An Enumeration of the Vascular Plants known from Suriname* (1906). This book was basically a checklist of 2101 species known to occur in Suriname. From the standpoint of ethnobotany and conservation, this publication was useful in that it gave vernacular names and noted which species were then believed to be endemic. Although there were 293 plants listed as occurring only in Suriname (and this figure has been used as recently by Toledo [1984]), subsequent collecting has revealed that many of these species also occur in adjacent countries.

Twenty-five years after the publication of this important initial work, Pulle (1932) initiated the *Flora of Suriname* series. Published under the auspices of the University of Utrecht, the *Flora* initially dealt solely with Suriname, but recent volumes have included data on both Guyana and French Guiana.

One factor that limited the scope of early botanical research was the colonial system. Each of the Guianas was tied to a different mother country and, unlike the situation in most of the Neotropics, neighboring countries did not share a common language. Furthermore, collectors in the Guianas usually worked only in a single country. Once colonial governments became interested in the economic potential of tropical timbers, however, forest services were set up to initiate research and development. The establishment of these forest services was important in fostering botanical research in all three of the Guianas (R. Cowan, pers. comm.).

One of the most useful works inspired by the interest in tropical timbers was *Bomenboek voor Suriname* by Lindeman and Mennega (1963), a well-illustrated forester's manual of the most important tree species. *Suriname Timbers* by Vink (1977) is a summary of the available information on major species of timber. Van Roosmalen's *Surinaams Vruchtenboek* (1977) is an excellent handbook of the fruits of the local flora, and a more recent version (1985) includes the fruits of all three Guianas. An excellent semipopular book on the orchids of Suriname was recently published (Werkhoven 1986).

Although it was founded recently (1946), the National Herbarium of Suriname contains over 19,000 specimens. Located at the National University just outside the capital city of Paramaribo, the herbarium is widely regarded as one of the best curated collections in South America. Furthermore, this collection will undoubtedly be greatly expanded as a result of the Flora of the Guianas project. A cooperative research effort by the University of Utrecht, the Smithsonian Institution, the New York Botanical Garden, the French office for overseas research (ORSTOM) and the governments of the Guianas, this thirty-year project will be the definitive work on the Guiana flora.

The vegetation of northern Suriname has been the subject of several in-depth studies (e.g. Lindeman 1953; Lindeman and Moolenaar 1959; Donselaar 1965; Schulz 1960). On the other hand, the Sipaliwini savannas are the only formation in southern Suriname that have been the subject of ecological and/or phytogeographical research (e.g. Donselaar 1968; Oldenburger et al. 1973). In fact, there have been very few collections made in southern Suriname (see Table 1). Outside of my ethnobotanical investigations, the only research on the rainforests of southern Suriname has been conducted by my colleague Fritz van Troon, a Saramaccaner Bushnegro in the employ of the Suriname Forest Service who established several study plots along the upper Sipaliwini river in early 1985.

THE INDIANS OF SURINAME

Five major tribes inhabit Suriname: the Akuriyos, the Arawaks, the Caribs, the Tiriós and the Wayanas. The Warao Indians lived in Suriname within historical times, but today exist only in Guyana and Venezuela. All of the tribes in Suriname today except for the Arawak are classified as members of Carib language group (Basso 1977; Durbin 1977).

The Indians of Suriname have long been divided into two categories—the "Benedenlandse Indianen" (the Indians of the coast) and the "Bovenlandse Indianen" (the Indians of the interior). Since the Europeans first landed and then settled on the coast and the lower reaches of the major rivers, the "Benendenlandse" Indians—the Caribs and the Arawaks—have been in almost constant contact with western society for several hundred years. The tribes of the interior—the Tiriós, the Akuriyos and the Wayanas—inhabit one of the most remote corners in all of South America, and it is only during the last quarter century (and even less for the Akuriyos) that these Indians have been in constant contact with the outside world via the presence of Protestant missionaries. Unlike the Indians of the coast—some of whom were involved to a significant degree with the plantation economy that characterized the colonial era in Suriname—the Indians of the interior

TABLE 1. COLLECTORS IN SOUTHERN SURINAME[1]

Name	Locality	Date	Numbers
H. E. Rombouts	Sipaliwini River and Sipaliwini savannas[2]	Aug/Oct 1935	193-560
J. F. Hulk	Sipaliwini savannas	1910-1911	35-80
D. C. Geijskes	Sipaliwini savannas	1952	---
G. J. Wessels Boer	Sipaliwini savannas	1963	688-700
J. V. Donselaar[2]	Sipaliwini savannas	1966	3523-3723
F. H. Oldenburger, R. Norde & J.P. Schulz	Sipiliwini savannas	1968-1969	1-987
G. M. Versteeg	Tapanahony River	Jul-Nov 1904	599-926
J. W. Gongrijp	Tapanahony River	Nov 1918	some numbers before and after 4175
H. E. Rombouts	Tapanahony River	Sept 1936 - Feb 1937	601-680
M. J. Plotkin	Sipaliwini River	Dec 1982 - Jan 1983	1-176
M. J. Plotkin	Sipaliwini River	Aug 1983 - Sep 1983	200-296
M. J. Plotkin & F. von Troon	Sipaliwini River	July 1984 - Aug 1984	300-487a
M. J. Plotkin & F. von Troon	Sipaliwini savannas	Aug 1984	487b-512
M. J. Plotkin & F. von Troon	Tapanahony River	Aug 1984	513-657

[1] Data on early collectors provided by F. Vermeulen, Institute of Systematic Botany, Utrecht.

[2] Donselaar (1968) subdivded the Sipaliwini savannas into five sections. The largest is the Sipaliwini savanna, which measures 63,000 ha and is by far the largest. Since the other four sections are much smaller and, since they all occur at the headwaters of the Sipaliwini River, for my purposes I lump them under the term Sipaliwini savannas.

have, for the most part, remained outside the cash economy. With the advent of missionaries, widespread acceptance of western religion (except among many of the Wayanas), and entrance into the market economy (working for the government, the church and wildlife exporters), many aspects of the traditional culture are changing rapidly or disappearing altogether.

As a whole, the tribes comprising the Carib language group have been relatively well-studied. By the mid-1970s extensive anthropological research had been conducted on twelve different tribes (Basso 1977) and good early ethnographic data were also available (e.g. von den Steinen 1884). Basso (1977) listed eight traits she considered "typically Carib," including four that entail some aspect of economic botany: (1) bitter manioc (*Manihot esculenta*) cultivation; (2) shamanistic rituals (often as a means of disease diagnosis and treatment); (3) pan-village communal ceremonies that are secular and commemorative in nature; and (4) use of tobacco as the principal means of inducing extraordinary experiences.

Of these four traits, all except manioc cultivation have been discouraged or eliminated as a result of missionary activities in the villages in which I worked. Although Kloos (1971) concluded that Carib societies have certain fundamental structural principles that resist outside influences, it is clear that the relationship between the Indians of southern Suriname and their ambient vegetation will undoubtedly change in the future as the Indians become less reliant on local plants as their sole source of medicines.

The first major study of Carib peoples in Suriname was Father Ahlbrinck's work with the coastal Caribs, which culminated in his *Encyclopaedie der Karaiben* (1931). Hoff lived with the Galibi Caribs for several years during the 1950s and has published two important papers on Indian languages (Hoff 1955; 1968). It should be noted that most of the ethnographic data on two of the southern tribes—the Tiriós and the Wayanas—have been collected outside of Suriname. Both tribes straddle borders—the Tiriós, Suriname-Brazil and the Wayanas, Suriname-French Guiana. Frikel (1960, 1961, 1971, 1973) has published extensively on the Tiriós in Brazil, while Hurault (1965a, 1965b, 1968) has published important data on the Wayanas of French Guiana. Within Suriname, the Tiriós were studied extensively during the 1960s by Rivière (1969, 1981). Butt (1970) has published data on the Suriname Wayanas, and Kloos has worked on the Akuriyos (1977a; 1977b). Recently, Rivière (1984) published an analysis of social organization among the Carib tribes of the interior region of the Guianas.

My study, then, represents an attempt to begin to fill a large gap. With the exception of a few passing references to what the Indians cultivate (e.g. Rivière 1969; Butt 1970) or collect in the wild (e.g. Kloos 1977a, 1977b), there have been no ethnobotanical studies of the Tiriós, the Akuriyos, or the Wayanas in Suriname (the ethnomedicine of the Brazilian Tiriós was studied

by Cavalcante and Frikel [1973]). These are three very different tribes: (1) the Tiriós–known to inhabit southern Suriname for many hundreds (if not thousands) of years; (2) the Wayanas–who moved into southern Suriname within historical times; and (3) the Akuriyos a possible Neolithic tribe. The challenge was to document the Indians' knowledge of the useful properties of local plants before this knowledge was irretrievably lost.

The Tiriós

The Tiriós (Fig. 2) have long been known to inhabit the Suriname-Brazil border region on the rivers Coeroeni, Tapanahony, and Palomeu in the north and the West Parú, East Parú and Marapí rivers to the south (Kloos 1972). Traditionally in villages of approximately 30 inhabitants, these settlements lasted for only several years before they were abandoned for another site (Rivière 1981). Like the Wayanas, the Tiriós practice slash-and-burn agriculture, cultivating manioc (*Manihot esculenta*), pineapple (*Ananas comosus*), papaya (*Carica papaya*), annatto (*Bixa orellana*), red peppers (*Capsicum* spp.) and tobacco (*Nicotiana tabacum*).

The missionary-anthropologist, Padre Protasio Frikel, who lived and worked among the Tiriós for many years, hypothesized that the tribe arose through four distinct stages of cultural development (Frikel 1961):

(a) **Stage I** – The earliest inhabitants of the Brazil-Suriname border area, the "Pre-Tiriyó," were cave-dwelling hunter-gatherers who used crude stone tools and who neither practiced agriculture nor made bows and arrows. This group appeared prior to the sixteenth century, yet Frikel claimed (somewhat correctly, it turned out) that certain persistent subgroups, like the Akuriyos, still lived at this primitive level.

(b) **Stage II** – An invasion of groups from the west during the sixteenth and seventeenth centuries conquered the original inhabitants of the region. The peoples of this stage used stone tools but practiced incipient agriculture, and they knew the bow and arrow.

(c) **Stage III** – The third stage, which began in the eighteenth century, involved an increasingly sophisticated form of agriculture (including cultivation of cotton, *Gossypium* sp.) and produced new types of huts, arms, and utensils.

(d) **Stage IV** – The current stage began at the turn of the century, when the Tiriós were contacted by people of both European (Brazilian, Dutch, American) and African (Bushnegro and Creole) descent.

According to tribal legends, the Tiriós originated on the top of a mountain on the Brazilian side of the border. This is probably Morro do Kantani, known also as Pico Ricardo Franco (2° 17′ N, 55° 56′ W). Rivière (1969) concluded that the Tiriós may be a mixture of several different groups. Pierre

Fig. 2. Tirió Indian hunter. Photo by M. J. Plotkin.

Grenand (pers. comm.), who has conducted extensive field research among the Indians in French Guiana, has suggested that the Tiriós may be a mixture of peoples who reached the Tumac-Humac range both from the north (the Caribbean) and the south (lower Amazonia).

Padre Cirilio Haas, a Franciscan priest who has for many years been working with the Tiriós in Brazil, told me of one of the Tirió "legends," which presumably relates to the origin of the tribe. The Tiriós tell of a time when their ancestors had to cross a land that was so cold that the people had

to wrap themselves in the skins of animals. This story was first related to Frikel in the late 1950s. One can only wonder whether this story represents a tribal recollection of crossing the Andes and/or the Bering Strait.

The first published record of the Tiriós may have been that of Cristobal de Acuña (1641). Acuña was a Jesuit who accompanied the Portuguese Pedro Teixeira on an expedition through Amazonia in 1639. On the island of Tupinambarana, the Indians gave a precise location for a tribe of female warriors: "they lived high up the Nhamundá or the Trombetas, beyond four other tribes. It was roughly the same location as [Gasper de] Carvajal's and [Bernard] O'Brien's: in the dramatic forested hills of Acari and Tumucumaque that form the watershed between the rivers flowing south into the Amazon or north into the Guianas" (Hemming 1978).

The Tiriós traditionally wear their hair down to their shoulders, and many of the men have features that are noticeably feminine. Hemming (1978) concluded that this combination of factors may have given rise to the legend of the Amazons.

The first recorded contact between the Tiriós and the Europeans was in the 1840s, with Robert Schomburgk on the upper "Wanamu" [=Anamu] river in Brazil (Schomburgk 1923). Contact prior to this report may have been made by the Portuguese who, aided by "Oyampi" [=Wayapi] Indian guides, were searching for slaves (Frikel 1971). It may have been these Portuguese slave traders who first introduced the diseases that have ravaged the Tiriós until relatively recently.

Crevaux (1883) recorded meeting Tiriós who had survived an epidemic in the northern part of Pará state. O. Coudreau came into brief contact with the Tiriós on the Rio Cuminá (O. Coudreau 1901; quoted in Frikel 1971). Three Dutch border expeditions - the Tapanahony Expedition of 1905, the Tumac-Humac expedition of 1907, and the Courantyne Expedition of 1910-11—entered the regions inhabited by the Tiriós (Rivière 1969). Reports by members of the expedition—particularly those of De Goeje—contain valuable ethnographic data (de Goeje 1908a; 1908b).

It was shortly after the last of these expeditions that Farabee (1924) traveled through southwestern Suriname. Although he visited two "Diau" [=Tirió] villages, his reports contain relatively few ethnographic data. In 1928, General Candido Rondon ascended the West Parú and found one group of Tiriós living on the Rio Marapí (Rondon 1953). Ten years later, a Brazilian boundary commission ascended the West Parú and met the Tiriós who were then living there (Aguiar 1943; quoted in Frikel 1971).

A most extraordinary census of the Tiriós was conducted by Lodewijk Schmidt, who crossed southern Suriname and ventured into Brazil during the early years of the second World War, searching for non-existent Japanese landing strips (Schmidt 1942). One of my informants worked as a guide for

Schmidt and remembers that Schmidt was the first black person the Indians had ever seen who was not a Bushnegro.

It was these Bushnegroes who served as an important buffer in keeping the Suriname Tiriós isolated from Europeans on the coast. Descendants of escaped slaves, the Bushnegroes established West African tribal lifestyles along major rivers in the Suriname interior during the eighteenth and nineteenth centuries (Price and Price 1980). When these settlements were established, the Tiriós retreated into the interior (Rivière 1969). The blacks developed a lucrative trading relationship, acting as brokers between the Europeans on the coast and the Indians in the south. The Bushnegroes brought machetes, matches, mirrors, and scissors (which they claimed to have grown on trees!) and traded them for bows, arrows, and hunting dogs. These blacks protected their monopoly by limiting travel to the interior by the colonists and by frightening the Indians with lurid tales of the bloodthirsty whites (Rivière 1969; Roth 1974).

Nevertheless, despite their limited contact with outsiders, the Tiriós were decimated by diseases. Crevaux (1883) provided the first report of an epidemic among the Indians, although these illnesses may have been brought in by the Portuguese much earlier. In 1952, an expedition was sent to the interior of Suriname by the Dutch to investigate rumors of an epidemic among the Indians (Rivière 1969). During the 1950s, a series of Dutch/American explorations in the Tumac-Humac range repeatedly introduced gonorrhea and other contagious diseases, which all but wiped out several villages (Frikel 1971).

Today, the Tiriós state that they knew they were dying out, and they knew that the diseases were the cause. Even the Bushnegroes were known to have been the carriers of these illnesses, though they were depended on by the Indians as sources of essential trade goods.

When the first missionaries came to the Tiriós in the late 1950s, the Indians were declining in number (Rivière 1969; Kloos 1977a; Frikel 1973). In 1959, the Brazilian Air Force cleared an airstrip on the Parú savannas and this site became the Roman Catholic mission under Franciscan missionaries known today as Pousoe Tirió. A year later, a mission station for the Tiriós was established by Protestants on Alalapadu Creek, a tributary of Wioemi Creek, which is itself a tributary of the Sipaliwini River in south central Suriname. Another mission was later set up at Palomeu to the east.

By the mid-1970s, fish and game resources in the vicinity of the Suriname missions had been seriously depleted by burgeoning populations. (The last time the Indians mounted a major fish-poisoning at Alalapadu, they caught only six fish!). This mission was then relocated on the banks of the Sipaliwini river in southwest Suriname. Most of the Indians in southeast Suriname now live in Tepoe, a mission station on the upper Tapanahony.

Because of the health care and schooling provided by the missionaries, these villages have acted as magnets, and today there are few if any satellite settlements of Tiriós on surrounding rivers. A similar state of affairs exists as Pousoe Tirió in Brazil.

The Wayanas

Of the three Indian tribes in southern Suriname, the Wayanas are undoubtedly the most recent arrivals, having entered the Guianas within historical times (Fig. 3). The original home of the Wayanas is located in the northeast Amazon, on the Jari and East Parú rivers (Hurault 1965b; 1968). During the eighteenth century, the Wayapi, a Tupian tribe, migrated from their ancestral lands (possibly the Rio Xingu in lower Amazonia) up to the Rio Jarí. Aided by arms supplied by the Portuguese, who had sometimes formed alliances with Tupian tribes during their conquest of Brazil (Hemming 1978), the cannibalistic Wayapi conducted a series of wars against several tribes. Among the Indians that suffered from their onslaught were the Wayanas, particularly when the Wayapi began moving north along the Rio Jarí (Grenand 1980).

After the Wayanas crossed the watershed into the Guianas, they moved in two directions: up the Litani River to the northwest and up the Maroni River to the northeast. That Bushnegroes were already present on the lower reaches of these rivers was probably a positive factor in inducing the Wayanas to settle there (Butt 1965). The Djuka Bushnegroes on the Tapanahony and the Boni Bushnegroes on the Litani provided vital trade goods, much the same as other Bushnegro tribes were doing for the Tiriós to the west.

Originally, the Wayanas may have been an inland people. When visited by Leblond in 1789 in the Jarí basin, their villages were located far from the main river, strung along a forest trail with each village approximately 8 km from the next (Hurault 1965a). A traditional village ranged in size from 15 to 70 people. Like those of the Tiriós, the villages lasted usually between five and six years although some persisted for as long as a decade (Butt 1970).

Once the Wayanas settled in the Guianas, they adapted to a riverine environment. Their villages were situated in a linear fashion along the banks of the river (Butt 1970). Unlike the Tiriós, who maintained extensive trails and journeyed predominantly on foot (e.g. Frikel 1973), the Wayanas did most of their traveling by canoe (Hurault 1968). Next in importance to the slash-and-burn cultivation, the major activity of the Wayanas was fishing (Hurault 1968). Indeed, one of the factors that the Wayanas have traditionally considered when choosing a site for the establishment of a new village is the proximity to rocks and rapids that would offer optimal bow fishing (Butt 1970). This characteristic is again in sharp contrast to the Tiriós and Akuriyos, to whom hunting is significantly more important than fishing (Frikel 1973; Kloos 1977a).

Fig. 3. The author collecting medicinal plants with Wayana shaman. Photo by M. J. Plotkin.

Like so many other American Indian tribes, the Wayanas were decimated by diseases, beginning with their initial contacts with peoples of both European and African descent. These diseases were rampant well into this century (Sausse 1951). In the mid-1950s, measles and tuberculosis reduced the Wayanas to less than 500 in number (Devillers 1983). In 1961, the French government established a medical program and restricted visits by tourists. The Protestant missionaries who worked with the Suriname Tiriós set up mission stations with medical assistance a year later (Butt 1965).

Early visitors to the Wayanas include Patris in 1766 and 1769, Leblond in 1789, Crevaux in 1877, Coudreau in 1887-88 and de Goeje in 1908 (Hurault 1968). Since they have long lived on or relatively near large rivers, however, the Wayanas never were as isolated as the Tiriós or Akuriyos. Once they moved into the Guianas, they lived closer to the Bushnegroes than the Tiriós ever did—in fact, there is actual overlapping of Boni and Wayana villages on the Maroni (Butt 1970).

Today, the Wayana number about 770, and their villages are located on both sides of the Suriname-French Guiana border on the upper Tapanahony, the Upper Lawa, and on the lower Litani and Maroni, both of which are tributaries of the Lawa. Their access to commercial goods, due to the proximity

of the French town of Maripasoela on the Lawa, is much greater than is the case with the Tiriós or the Akuriyos. Nevertheless, they are a very proud people, and seem to have a stronger sense of cultural identity than the other two tribes in southern Suriname.

The Akuriyos

In June of 1968, a group of Wayana Indians were canoeing down the Waremapan Creek, a tributary of the Litani River in southeastern Suriname. Although they were en route to their villages on the Lawa River to the north, they beached the canoes to give chase to what they took to be a herd of peccaries. What they found was at least a partial solution to a long-standing anthropological mystery—the identity of the "Lost Tribe of Suriname"—the Akuriyos (Fig. 4).

As early as the 17th century, there were reports of a tribe known as the "Acooroes" inhabiting the upper reaches of the "Marrawini" (=Marowijne) River (Harcourt 1928). In the late 1800s, Crevaux heard of a tribe known as the "Wayarikure" (Wayana name for the Akuriyos), but never met them (Riviere 1969). De Goeje, a member of the Brazil-Suriname boundary commission, published a map (1908a), which correctly placed the "Oyaricoulet" between the Oranje and Tumac-Humac mountains. In 1937, a small group of Akuriyos was found by a Dutch border expedition on the Oelemari river in SE Suriname. Contact was maintained only for a very short period before the Indians disappeared into the forest (Meuldijk 1939; quoted in Kloos 1977a).

As a follow-up to this meeting, the Dutch government sent an expedition to the region under the leadership of Ahlbrinck, the missionary who had conducted extensive field research among the coastal Caribs. Ahlbrinck was able to maintain contact for only a day and a half before the skittish Indians once again disappeared into the forest. Although these people were undoubtedly the Akuriyos, Ahlbrinck (1956) identified them as the "Wama." According to von Reis and Lipp (1982), there is a single specimen of *Calathea* in the New York Botanical Garden Herbarium (1939/G. Stahel No. 38) with the annotation "Main carbohydrate food of the wild Wawa [=Wama] Indians (without agriculture!) on the upper Oelemani [=Oelemari] River." This specimen was collected presumably during the Ahlbrinck expedition and constitutes probably the first recorded information on the ethnobotanical lore of the Akuriyos.

In 1953, the Dutch government sent another expedition to contact the Akuriyos. Although evidence of recent habitation was found, no contact was made. From 1965 on, the American West Indies Mission in Suriname organized a series of expeditions to search for the Indians, but their initial efforts were unsuccessful (Kloos 1977a). When contact was finally established by the

Fig. 4. Akuriyo boy with pet peccary.

Wayanas in 1968, the Akuriyos were living as true hunter-gatherers; they did not practice any form of agriculture, they carried stone axes, and they did not know how to make fire (Schoen 1969).

At the time of their "re-discovery," the Akuriyos inhabited the region of the headwaters of Loe Creek, the Litani River, and the Oelemari River (all tributaries of the Lawa River), the Pimba and Walimeroe rivers (tributaries of the Tapanahony River) and they occasionally crossed into Brazil (Kloos 1977a). They lived in bands ranging in size from two to thirty individuals. Palm fruits (particularly *Mauritia flexuosa, Oenocarpus bacaba* and *Astrocaryum* spp.) were important components of their diet, which was rich in protein (due to a heavy consumption of meat), yet poor in carbohydrates—an unusual condition among Amazonian natives. Not having access to sugar cane (*Saccharum officinarum*), which is ubiquitous in Tirió and Wayana villages, the Akuriyos had a strong craving for carbohydrates, as evidenced by their being able to distinguish 35 different kinds of honey (Kloos 1977a). So strong was the craving for honey among the Akuriyos that falling out of trees while searching for bees' nests was the leading cause of death among adult males (Kloos 1977b).

It is interesting to note that a major motivation behind the Akuriyos' continuous trekking was not so much the lack of food as it was the certain

need for material goods. In such a sparsely populated region as southeast Suriname, game is rather abundant, but it was the stone for axe heads (found only in streams near the Oranje mountains) and the arrow cane (*Gynerium sagittatum*) for arrow shafts that they needed.

The question has been raised as to whether the Akuriyos are truly "Neolithic" in their development. Kloos (1977a,b) believed that they are not, hypothesizing that they have "devolved" from a sedentary lifestyle (which included cultivation of *Manihot*) because of intervillage conflicts. If Kloos' theory is correct, the adoption of a hunter-gatherer lifestyle may have been undertaken as an adaptation to escape Portuguese slave-traders or to reduce the threat of introduced diseases that are known to have decimated aboriginal tribes in southern Suriname (Crevaux 1883; Rivière 1969). This would help also to explain hostility to outsiders. The Akuriyos shunned other peoples, going so far as to kill Bushnegroes who strayed into their territory (unlike the Tiriós, who usually welcomed the Bushnegroes as sources of otherwise unattainable trade goods). Like the recently contacted Waorani of Ecuador (e.g. Davis and Yost 1983), the Akuriyos avoided all major rivers and did not know how to swim or build canoes. Their isolation was further reinforced by their suspicion and hostility to members of other Akuriyo bands. As is the case with other South American Indians (e.g. Schultes 1975; Reichel-Dolmatoff 1975), the Akuriyos sometimes attributed killings by jaguars to the work of evil shamans of a rival group (Kloos 1977b).

At this point in time, all of the Akuriyos are said to have given up their hunter-gatherer existence and are living in Tirió villages. There are two Akuriyo men living in Kwamalasamoetoe; both have Tirió wives. The rest of the Akuriyos, approximately 50 in number, live in Tepoe, where they are a distinct minority. Consequently, from a cultural standpoint, the Akuriyo children are being raised as Tiriós, since the latter are clearly the dominant group in terms of both number and language. The future of the Akuriyos as a distinct cultural entity is indeed gloomy.

In 1969, the noted anthropologist Peter Rivière published a book on the Tiriós that included the statement: "My inclination is to place [the Akuriyos] with the other extraordinary people who dwell in the Tirios' imagination."

It was at about the time this statement was being written that the Wayanas "found" the Akuriyos. Many field biologists working in South America had heard "wild" Indians living nearby: I was no exception. Several years ago, one of the Tiriós was hunting approximately 2 km upriver from Kwamalasamoetoe when he came face-to-face with a group of unfamiliar Indians. He greeted them in several languages, yet they did not seem to understand him. They became frightened and fled into the forest. The Tirió returned to Kwamalasamoetoe and assembled a search party. When they returned to the area, the Indians found footprints but were unable to make further contact.

ETHNOBOTANY: THE URGENT NEED FOR MORE RESEARCH

What is the future of these Indian tribes as cultural entities? In my opinion, it is relatively bleak in many respects. With the advent of Western religion and medicine, the traditional role of the shaman has been usurped. Almost all of the Indians visit the missionaries' clinics when they are ill. Consequently, the ethnobotanical lore of the tribe—the results of thousands of years of trial and error with the local flora—is not being passed on to the younger generation. Virtually none of the shamans with whom I worked have an apprentice.

The situation is similar in many other regions. As tribal peoples become more dependent on introduced goods (medicines, foods, shotguns, etc.), they reduce their dependence on tropical forest plants. There exists an urgent need to expand ethnobotanical research in all of the tropical forests of the world. If we do not do so, a great deal of ethnobotanical information will be irretrievably lost in the near future. This concept was succinctly stated by the great Harvard ethnobotanist Richard Evans Schultes (1963):

> Civilization is on the march in many, if not most, primitive regions. It has long been on the advance, but its pace is now accelerated as the result of world wars, extended commercial interests, increased missionary activity, widened tourism. The rapid divorcement of primitive peoples from dependence upon their immediate environment for the necessities and amenities of life has been set in motion, and nothing will check it now. One of the first aspects of primitive culture to fall before the onslaught of civilization is knowledge and use of plants for medicines. The rapidity of this disintegration is frightening. Our challenge is to salvage some of the native medicobotanical lore before it becomes forever entombed with the cultures that gave it birth.

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PRIMATE CONSERVATION: A STATUS REPORT WITH CASE STUDIES FROM BRAZIL AND MADAGASCAR

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Primate populations in the wild are decreasing worldwide. Three major factors contribute to the decline of these populations: habitat destruction, hunting, and live capture for export or the local pet market. Non-governmental conservation organizations are working together with indigenous country governments to counteract these pressures through grassroots education efforts, technical information exchange, research, and training of in-country conservation biologists. Conservation efforts in Brazil and Madagascar, two areas we consider to be among the highest priorities for primate and tropical forest conservation in the world, are reviewed.

We would like to follow this publication's main theme of conservation of biological diversity in the tropics. Our focus, however, will be on what have been called the "charismatic megavertebrates." Much of wildlife conservation grew out of a desire to save some of the world's most spectacular mammals, and in many ways these animals still best convey the concept of conservation to the general public. In this paper we discuss conservation problems and current World Wildlife Fund (WWF) projects on one group of charismatic megavertebrates—the nonhuman primates.

It has become increasingly obvious in the past few years that wild populations of most nonhuman primates are decreasing all over the world. Several species, like the mountain gorilla (*Gorilla gorilla beringei*) from Rwanda, Uganda, and Zaire; the golden lion tamarin (*Leontopithecus rosalia*) from Brazil; and the lion-tailed macaque (*Macaca silenus*, Fig. 1) from south India, are dangerously close to extinction. Others, like the pygmy chimpanzee (*Pan*

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Fig. 1. Lion-tailed macaque (*Macaca silenus*), an endangered species from South India. Photo by Russell A. Mittermeier.

paniscus) from Zaire, the orangutan (*Pongo pygmaeus*) from Borneo and Sumatra, and the woolly monkeys (*Lagothrix* ssp.) from Amazonia, are disappearing at an alarming rate. Some, like the rhesus monkey (*Macaca mulatta*) from India and the capuchins (*Cebus* spp.) from South America are still abundant, but declining in many parts of their range. Only a few highly adaptable species appear to be maintaining steady populations. These are mainly small, rapid-breeding monkeys such as the squirrel monkeys (*Saimiri* spp.), the golden handed tamarin (*Saquinus midas midas*), and the pygmy marmoset (*Cebuella pygmaea*), all found in the vast Amazon forests of South America (Mittermeier 1982).

There are three major threats to primate populations: destruction of habitat, hunting for food and other purposes, and live capture for export or to serve the local pet market. However, the primary reason for the disappearance of primates is without a doubt the destruction of the world's tropical forests. More than 90% of all primates are found in the tropical forests of Asia, Africa, and South and Central America. These forests are being destroyed at a rate of 10-20 million hectares per year (U.S. Interagency Task Force 1980), the latter figure translating to an area about the size of the state of California being clearcut every two years. The forests are cut for timber, charcoal, and firewood; they are burned and cleared for agriculture and pastureland; or

they are flooded by massive hydroelectric projects. As the forests are destroyed, so are the animals that live in them.

Hunting is the next most important reason for the disappearance of wild nonhuman primate populations. Primates are killed for a variety of reasons, but most often as a source of food. The effects of hunting vary greatly both regionally and from species to species. For instance, hunting is not very prevalent in India, where monkeys are associated with the monkey god, Hanuman. Nor is it significant in Muslim countries, where primates are considered unclean and not fit for consumption. However, primate hunting in at least three parts of the world—the Amazon region of South America, and West and Central Africa—constitutes a serious threat (Mittermeier 1982; 1987; Fig. 2). Primates are a major source of food in these areas, where they are frequently sold in the local markets.

Hunting does not affect all species equally. In Amazonia, for example, the larger species, such as woolly monkeys (*Lagothrix* spp.) and spider monkeys (*Ateles* spp.), are heavily hunted. The smaller ones, such as the squirrel monkeys (*Saimiri* spp.) and tamarins (*Saguinus* spp.) are ignored, as they offer too little meat. Hunting pressure on some species, such as *Lagothrix* and *Ateles* in Brazil and Peruvian Amazonia, is so intense that it has resulted in local extinctions, even when suitable habitats remain (Mittermeier and Coimbra-Filho, 1977; Soini 1982).

There are many other reasons why primates are killed by humans. Some are hunted to obtain their skins or other body parts for ornamentation. A striking example of this is the use of black and white colobus monkey (*Colobus guereza*) skins to make cloaks and headdresses for native Africans, and rugs and coats for tourists. From 1880-1900, some two and one-half million colobus skins arrived on the European continent, where they were used to make capes, muffs, and rugs. Colobus skin rugs were sold in East African tourist shops until as recently as 1978 (Mittermeier 1973; Oates 1977).

In Africa and Asia, primates (especially baboons, *Papio* spp. and macaques, *Macaca* spp.) are hunted because they are considered agricultural pests. Normally these animals are killed by local people using sticks, rocks, or poisons. However, occasionally the crop raiding is so intense and destructive that major eradication efforts are undertaken. As an extreme example, the government of Sierra Leone sponsored monkey drives from 1948 to 1962 to rid the agricultural areas of primates. Government records show that 245,513 primates (an average of 19,000 per year) were destroyed in these raids (Tappen 1964).

Occasionally primates are killed as bait. In remote areas of the Amazon region, cat hunters use larger species like woolly monkeys and spider monkeys to bait traps for jaguars and ocelots. The cats are caught alive in these traps and then either shot in the head or strangled, which gives the hunter a

Fig. 2. Capuchin monkey shot for food in southern Suriname. Photo by Mark J. Plotkin.

more valuable skin without bullet holes (Mittermeier and Coimbra-Filho 1977). In addition, some species, most often chimpanzees and gorillas, are maimed or killed by traps set for other animals (Fossey 1983; Ghiglieri 1984).

The third important reason for the decline of primate populations is live capture, either for the pet or research market. Live capture of primates is less a factor in the total decline of primate populations than is habitat destruction or hunting. However, for certain endangered species that are in heavy demand, it can be very serious. Species populations that have declined due to the export trade are the chimpanzees (*Pan troglodytes*) from Africa and the cottontop tamarin (*Saguinus oedipus*) from Colombia (Hernandez-Camacho and Cooper 1976; National Institutes of Health 1978; IUCN 1982). In addition, the woolly monkey's (*Lagothrix lagotricha*) popularity as a pet in Amazonia has contributed to its decline in the wild. Unfortunately, for every primate that is captured live, at least one other is normally killed. This is because the infants, the easiest to obtain, tame, and transport, are captured by shooting the mother and removing the baby.

If present trends in the decline of primates continue, we stand to lose a substantial percentage of the world's primate species in the near future. Of the roughly 200 species currently recognized, about one in every three is already considered endangered, vulnerable, or rare by the International

Union for Conservation of Nature (IUCN), and about one in every seven are highly endangered and could be extinct by the turn of the century. Furthermore, these are minimum estimates as the exact status of many species is not known.

In 1977, the Primate Specialist Group of the IUCN responded to the critical situation facing nonhuman primates by producing a comprehensive document called the *Global Strategy for Primate Conservation*. In this strategy, the authors emphasized two goals: (1) ensuring the survival of particular endangered species, such as the mountain gorilla, wherever they happen to occur; and (2) providing effective protection for large numbers of primates in areas of high diversity and abundance.

The Global Strategy attracted much attention from conservation organizations, subsequently leading to the creation of the World Wildlife Fund Primate Program and a substantial increase in support for primate conservation projects. Since its inception in 1978, the program has funded more than 100 projects, both large and small, in 32 different countries (Fig. 3). It also produces and distributes the combined journal and newsletter, *Primate Conservation*, which serves as a major means of communication for the world's primate conservationists. In 1985, the program also launched a five-year Global Primate Conservation Campaign to raise at least one million dollars for primate conservation by the end of this decade.

Two important areas that are focused on in the Global Primate Conservation Campaign are the Atlantic forest region of eastern Brazil and the island of Madagascar. Habitat destruction in these areas is intense. In fact, so much forest has already been destroyed that further loss of habitat will have grave consequences for the remaining primate populations.

One of the main goals of the campaign and the conservation community as a whole is the maintenance of our planet's biological diversity. It is an established fact that a major portion of this diversity is found in the world's tropical forests. Brazil, with 360 million ha of tropical forest, is by far the most important country in the world for conservation of this biome, and the Atlantic forest region is the most endangered part of the Brazilian forest. Brazil is also the richest country in the world in terms of primate diversity, with a total of 53 species recorded thus far (Table 1).

The Atlantic forests in eastern Brazil are a unique series of ecosystems quite distinct from the extensive Amazonian forests to the northwest. They once stretched fairly continuously from the state of Rio Grande do Norte at the nose of South America to as far south as Rio Grande do Sul, the southernmost Brazilian state (Fig. 4). This area included some of the richest, tallest, and most beautiful forests on earth. However, this region was the first part of Brazil to be colonized, and it has been developed into the agricultural and industrial center of the country. Within its borders are two of the three

Fig. 3. Locations of Primate Program Project since 1979. Key: lighter circles = Primate Action Fund (small projects); darker circles = large projects.

TABLE 1. PRIMATE ENDEMISM IN THE WORLD'S TOP 15 COUNTRIES FOR PRIMATES

Country	No. Species (No. Endemic Species)	No. Genera (No. Endemic Genera)	% Endemic Species	% Endemic Genera
Madagascar	28 (26)	13 (12)	93%	92%
Indonesia	27-30 (12-15)	8 (1)	44-50%	12.5%
Brazil	53 (18)	16 (2)	34%	12.5%
Colombia	27 (3)	12 (0)	11%	0%
Peru	27 (2)	12 (0)	7%	0%
Zaire	29-32 (2)	13-15 (0)	6-7%	0%
Nigeria	23 (1)	13 (0)	4%	0%
Cameroon	28-29 (0)	14 (0)	0%	0%
Congo	22 (0)	14 (0)	0%	0%
Equatorial Guinea	21-22 (0)	12 (0)	0%	0%
Central African Republic	19-20 (0)	11-12 (0)	0%	0%
Gabon	19 (0)	11 (0)	0%	0%
Uganda	19 (0)	11 (0)	0%	0%
Bolivia	17-18 (0)	11-12 (0)	0%	0%
Angola	18-19 (0)	10-11 (0)	0%	0%

largest cities in South America—Rio de Janeiro and São Paulo—the latter being one of the largest cities in the world. The result has been large-scale forest destruction in order to produce lumber and charcoal and to make way for plantations, cattle pastures, and industry. We estimate that only about 1-5% of the original forest cover remains in eastern Brazil (Mittermeier 1982).

As might be expected, animal populations native to the Atlantic forest region are experiencing serious declines. For instance, 21 species and subspecies of monkeys are found in the Atlantic forest, and the studies that we have been conducting there since 1979 indicate that 14 of these taxa are already endangered and several are, literally, on the verge of extinction. Of the 14 endangered monkeys, 13 are found nowhere else in the world. In fact, 35% of Brazil's primates are endemic, which is the highest percentage in South America, and quite high worldwide.

The two most spectacular species of the Atlantic forest region are the golden lion tamarin (*Leontopithecus rosalia*, Fig. 5) and the muriqui (*Brachyteles arachnoides*, Fig. 6). These are also among the most endangered. The muriqui provides a good example of the use of charismatic megavertebrates to promote conservation.

The muriqui is the largest and most apelike of the New World monkeys.

Fig. 4. Original extent of the Atlantic forest region of eastern Brazil.

It is the largest mammal endemic to Brazil and, as such, provides an excellent symbol for the Brazilian conservation movement. It could very well become for Brazil what the giant panda is for China. To achieve this, WWF has launched a grassroots campaign for the muriqui in conjunction with the Brazilian Conservation Foundation, the Federal University of Minas Gerais, and the Rio de Janeiro Primate Center.

Fig. 5. The golden lion tamarin (*Leontopithecus rosalia*), an endangered species from the Brazilian state of Rio de Janeiro. Photo by R. A. Mittermeier.

Fig. 6. Muriqui (*Brachyteles arachnoides*), largest of the Neotropical monkeys and restricted to a handful of localities in the Atlantic forest region of eastern Brazil. Photo by Russell A. Mittermeier.

In order to increase public awareness of these animals, we are giving lectures in the cities and the interior, developing museum exhibits, and distributing T-shirts, stickers, and posters (Fig. 7) as well as a variety of educational materials. We have succeeded in obtaining considerable press coverage for the muriqui, including the production of a special World Wildlife Fund film that has now been translated into Portuguese for use on Brazilian television. We are also supporting various research projects on the ecology and conservation of the animal.

Fig. 7. Poster depicting the muriqui, used in the Muriqui Campaign in eastern Brazil.

A good indication of the success of our efforts is the fact that although the muriqui was a virtually unknown species in Brazil five years ago, it has now become so popular that it graces the cover of a Brazilian phone book, appears on two Brazilian postage stamps (Fig. 8), and is frequently in the Brazilian press and on television.

Additional WWF efforts in the conservation of the Atlantic forest region include projects on other mammals such as the endangered maned sloth (*Bradypus torquatus*), and on several bird species. We are also helping to improve management practices in several key parks and reserves, developing a conservation education curriculum for elementary schools, and organizing a wildlife training program at one of the best universities in eastern Brazil. We are developing links between Brazilian and American zoos by bringing some of our Brazilian counterparts to the U.S. for doctoral level training, and we support several key institutions in Brazil, most notably the Brazilian Conservation Foundation.

Overall, these efforts have led to a general increase in conservation awareness within Brazil, and we are hopeful that this new insight will help to save what remains of the Atlantic forest region and its spectacular biota.

Switching continents now, we move to the island of Madagascar, located only about 400 miles off the east coast of Africa. The island has been isolated from other land masses for at least 30-40 million years. For this reason, though Madagascar is little larger than the state of California, its biota is so unique that the island can be considered a separate biogeographical region. Although Madagascar ranks only 19th in the world for total forest cover, it has high levels of species diversity and very high species endemism. For example, Madagascar ranks fourth in the world for primate diversity and has the highest primate endemism (93%) of any country on earth (Table 1).

Fig. 8. Muriqui stamps from Brazil and Peru.

Malagasy primates are not the monkeys and apes that we usually envision when we think of primates. They are lemurs, a primitive group that occurs on Madagascar and nearby islands. The extant lemurs include more than 40 different species and subspecies ranging from the mouse lemur (*Microcebus murinus*), which is the smallest of the living primates, to the indri (*Indri indri*, Fig. 9), which is as big as a medium-sized dog and moves by bouncing from tree to tree like an arboreal kangaroo. Perhaps the most notable lemur is the aye-aye (*Daubentonia madagascariensis*), one of the most unusual mammals on earth and the only living representative of an entire primate family. The Daubentoniidae.

Other unique Malagasy wildlife includes the chameleons, which reach their greatest diversity there; the spectacular day geckos, which are among the most beautiful of all lizards; the tortoises, which include some striking species like the radiated tortoise; the couas, a group of birds found only in Madagascar; seven species of baobabs; and the Didiereaceae, a cactus-like family of plants unique to the island.

The spectacular fauna and flora of Madagascar is severely threatened by habitat destruction and, in some places, by hunting. What little forest remains is being chipped away by slash-and-burn agriculture and by removal of firewood and charcoal.

Fig. 9. The indri (*Indri indri*) of the eastern rain forest of Madagascar. Photo by Russell A. Mittermeier.

People arrived in Madagascar between 1,500 and 2,000 years ago and, in the ensuing 500-1,000 years, there followed a wave of extinctions of a large portion of the island's fauna. Among the species that were lost are the elephant birds (*Aepyornis* spp.), which were the largest birds that ever lived and had eggs that weighed 20 pounds; a pygmy hippopotamus (*Hippopotamus lemurlei*); an aardvark (*Pleistocteropus madagascariensis*); and six genera of lemurs, including animals like *Megaladapis*, which moved like a huge koala bear and grew to be as large as a female gorilla. Most of the species that have disappeared were larger than the surviving lemurs. If this extinction trend continues, the indri, which is the largest, and the sifakas (*Propithecus* spp.), which are the next in size, will be the next to go. In fact, several of the large lemurs are already highly endangered. Because of its uniqueness and the many threats it faces, we feel that Madagascar must be considered the single highest conservation priority in the world.

To prevent the disappearance of these animals and their habitats in Madagascar, WWF plans to apply some of the techniques learned in Brazil and other parts of South America to the situation there. We are also formulating an Action Plan for Madagascar that discusses priority conservation areas and species and recommends research, management, and implementation projects. We have plans to develop several new projects, and we are in the process of beginning a major fund-raising effort for Madagascar during the next year. In November, 1985, a special conference to develop a National Conservation Strategy for Madagascar was held in the capital city of Antananarivo. The conference succeeded in generating substantial enthusiasm for, and interest in, conservation, both within the country and on the part of many international organizations.

With this growing interest in conservation in Madagascar, we believe that it is not too late to turn the tide of habitat destruction to ensure conservation of a cross-section of endemic species and ecosystems.

In closing, although the current outlook for the survival of many of the 200 species of primates hangs in the balance, programs like the ones under way in Brazil and Madagascar offer some hope for the future. If these efforts can be continued and expanded, and if similar programs can be developed in other high priority regions, we believe it will be possible to save representative populations of all living primate species.

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THE CONSERVATION OF BIOLOGICAL DIVERSITY: THE CASE OF COSTA RICA IN THE YEAR 2000

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The irrational use of natural resources, often fostered by transnational enterprises, and ever-growing populations are the main threats to conservation in underdeveloped countries. The world community of conservationists must view these threats as increasing trends. Besides obtaining funding to establish protected areas, they must reinforce the institutional capacity and human resources for those areas and contribute to endowments that guarantee the perpetuation of conservation efforts. Conservationists and scientists must unite to promote environmental education programs, develop and teach agroecological practices that increase the yield of small parcels, educate on demographic aspects and, most importantly, interact with the Latin American communities who are the direct beneficiaries of the protected lands and the philosophy behind conservation.

Conservationists must routinely interact with decision makers at all levels in those countries and emphasize ecodevelopment. It is imperative that there be a commitment to the future as well as to the present investment in protecting biological diversity.

The need to conserve natural areas in pristine condition is not under scrutiny. Most nations do conserve natural areas. They do it for various reasons and they do it for the most diverse kinds of justifications. But underlying these justifications is the widely recognized need to keep and preserve entire ecosystems in form and function, rather than to preserve isolated organisms. Biological diversity is the password in today's conservation.

Because the greatest diversity of communities and organisms, about 60% of the world's biota, is in the tropics, which make up about 6% of the world's land area, conservation efforts are well directed to these regions. Fortunately for us all, big grantors are becoming aware of this fact and are showing more interest in saving those resources.

Few nations in the world, least of all the developing tropical countries,

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have sufficiently large and well-managed systems of protected areas. In fact, the number of areas under some sort of protection amounts to only 2-3% of the earth's surface and approaches 2500 parcels, equivalent to several hundred million hectares of preserves. However, tropical underdeveloped countries have increased their preserves in the last couple of decades. Some countries in Latin America boast that no less than 8% of their territory is under protection. Setting aside preserves has generated serious management problems because of inadequate human, financial, and technical resources. The Costa Rican government alone set aside 10% of its 51,000 square kilometers as national parks and preserves. I do not include acreage devoted to forestry, wildlife, and hydrologic reserves, which increases that figure to almost 25% of the national territory. Recalling that Costa Rica established its first national park in 1972, we must admit this is a remarkable accomplishment for such a small, impoverished country.

Where does Costa Rica go from here? I planned to use Costa Rica as a hypothetical showcase for the year 2000. I still will, but to a lesser extent because it is dealt with in greater detail in another paper (see Gamez and Ugalde, this volume). Today less than 20% of the forests in Costa Rica are relatively undisturbed. Nearly 20,000 hectares are deforested annually. Before the year 2000, perhaps even earlier, I believe there will be no forests like those many of us have seen in our lifetimes. In just 15 years, or less, this once heavily forested country will be importing wood for building and industrial purposes. In this sea of deforestation, the green islands of the national parks will be like gems that will translate, in the eyes of society, to millions of square boardfeet of building materials and will certainly be the targets of a needy and much larger population.

In 1983 the population of Costa Rica was 2.6 million. Today it is closer to 3 million. With an unofficial growth rate of nearly 3%, the Costa Rican population will double in ten years. This does not take into account the influx of thousands of refugees from the politically restless countries of Central America, who view Costa Rica as a haven of prosperity and stability. In 15 years, I predict that Costa Rica will have one million needy and hungry squatters, a vast majority of whom will be of mixed nationality. Unlike the Costa Ricans of the early 70s who left their expropriated lands peacefully and were relocated in strange areas to start anew, squatters will neither understand nor accept the need to maintain parks to protect the birds, the flowers, and the rivers. It will not be easy to keep a burgeoning population from protected areas when they learn, or are told, that at least 40% of such areas will yield some crop under intensive use, albeit one crop of maize by the slash-and-burn technique. Today, in Costa Rica, the threshold of productivity for arable lands and forest resources is about to be surpassed in most of the regions where such activities take place. This is not an exceptional case, if we

look at the following averages obtained recently by Brent Bailey of the Nature Conservancy. In Central America and Mexico, the average rate of deforestation is 275,000 ha/year. In the Greater Antilles (excluding Puerto Rico), it is 15,800 ha/year. In South America (excluding Southern Cone), it is 96,000 ha/year. Some countries have higher figures when considered individually. Assuming a conservative population growth rate of 1.5% per year, Central America will have over 200 million inhabitants, the Caribbean Basin 50 million, and South America will have 390 million persons. What we are talking about here is the fastest possible rate of aridization a continent has ever seen and mass biological extinctions unlike that of any other geologic period.

My contention, with Costa Rica in mind and as part of my duty as conservationist, is that we should proceed cautiously. Let us not put all our "papayas" in one basket, if I may be allowed to tropicalize and paraphrase. We have to spread our papayas to minimize the risks of all going bad. The papaya, because of its very perishable nature, provides an excellent portrayal of the condition of conservation in many tropical countries. Again, with Costa Rica in mind, how do we know when to stop land acquisition and concentrate on efficient management and perpetuation of the initial commitment? The answer is not a new one. It has been circulating for many years. It is Kenton Miller's concept of "ecodevelopment," which for Costa Rica is addressed in the paper by Gamez and Ugalde (this volume).

Enough said about the growth and needs of populations, the political uncertainty in some countries, and depletion of natural resources. Let me return to my grim, pessimistic scenario. What can we do? Is there hope for conservation and for conserved areas? Yes! There is hope. However, it is not simple and it is not without its price. I direct my message to two different groups of people; regretfully, these groups do not interact often enough.

The first group is conservation organizations. They can help solve the dilemma of the year 2000 in the following ways:

(1) Beyond acquiring and setting aside parcels of land, they must devote both time and money to develop institutional support that guarantees the perpetuation of the effort. For this they must invest in individuals who can best represent their interests at the highest possible levels of governmental decision-making.

(2) These organizations must also help build institutions to monitor the situation of in-country conservation and act as information brokers at all levels. One hectare of land without the appropriate infrastructure equals zero in conservation efforts. Any effort to save one million hectares without such support equals total disaster.

The second group is the scientists. What role can we play beyond pointing out which areas are suitable for conservation (often based on rather narrow reasons)?

(1) We can approach governments and national granting organizations and explore ways to increase productivity of the small farm, the typical 5-10 acre parcel of our campesinos. This should be done through less grandiose schemes than the green revolutions, with more attention to the logical management of available resources.

(2) Beyond the learned considerations from our important symposia, are we actively doing anything to approach zero population growth? Do we need to embrace radical measures, or can we come to a golden mean and persuade governments and people about the advantages of moderate population growth?

(3) Beyond our own everyday use of parks and protected areas as open laboratories for our research, are we willing to produce guides and literature that would enhance the enjoyment of those areas by the local population? By engaging in such activities we help to educate and instill a sense of wonder and appreciation in our natural heritage. Thus, the idea that parks are fancy, unnecessary things can be replaced by a realization that parks are nature's treasure chests that can be enjoyed through a better understanding. Should we not teach others what we have learned from our own close contact with nature?

Some of these suggestions may sound provocatively too political and as such may be viewed by many as taboos. You have been told not to interfere in the internal affairs of other countries when you travel abroad. Perhaps we need not pound on the President's door or lead a public demonstration. We can, however, approach the right people and make them our spokespersons. We must face the fact that many protected areas are the result of political maneuvers and through political manipulation they may also disappear. In many countries, half a million votes in one direction or another can drastically affect the alignment of a political party with respect to conservation issues. Usually these votes do not come from the educated voters. They spring forth from the ranks of the underprivileged, the illiterate, the campesino without land, the urban unemployed. If we do not educate those segments of the population and impress upon them the need to protect natural resources, the future of our beloved parks is threatened.

At this point, you might ask, why conserve? If it is so grim a picture, why bother? I believe in conservation when conservation is well designed, and when it is on a par with development. With every dollar or peso or colon invested in lands, there must be an equivalent investment in institutional and human resources to manage the areas. Yes, there is hope, as much hope as we are willing to muster through participation. Let us not burden a country with the problem of a tract of land whose management is beyond the means of that country. We must view inventory, selection, design, management,

and stewardship, from two perspectives–that of today and that of years from now. I believe that is the key to success in tropical conservation. Commitment to the myriad aspects of environmental education, population growth, home economics, agroforestry, politics, are all needed for the establishment of a park or bird sanctuary. Remember that in conservation issues we are all citizens of one, shared planet.

COSTA RICA'S NATIONAL PARK SYSTEM AND THE PRESERVATION OF BIOLOGICAL DIVERSITY: LINKING CONSERVATION WITH SOCIO-ECONOMIC DEVELOPMENT

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The congruency of conservation with social and political values has allowed Costa Rica to develop an exemplary system of national parks and reserves. Nevertheless, the country is facing increasing pressures on its natural resources and serious environmental deterioration, which not only affect its socioeconomic development, but threaten its park system. The preservation of biological diversity cannot be seen as unrelated to the social and economic needs of the country, which must be satisfied through a rational use of its natural resources. The magnitude and complexity of the problem of preserving tropical biological diversity is such that its solution can only be attained with the cooperation of developed nations.

For centuries Costa Rica has been a naturalist's paradise. Descriptions such as "...for its size, Costa Rica has more species than any other land mass of the planet..." (Kaizer 1985) are frequent. Or: "The country is a biogeographical land bridge in the isthmus of the Americas, a topographically diverse country where the flora and fauna of North and South America meet" (Beebe 1984). "Three factors make Costa Rica ecologically rich; its geographical location, its climate, and its topography. Two oceans bathe its shores, and high mountains form a backbone down its center. The highest peak in Central America soars 12,500 feet above sea level, rising from dense rainforests to a fairyland of glacier-carved lakes and subalpine meadows. In the lowland plains of both coasts and the undulating folds of Costa Rica's mountain ranges, diverse species from all over the Americas have intermixed, and new species have sprung forth, creating what is an astonishingly rich flora and fauna" (National Parks Foundation 1983). Costa Rica's natural wealth has attracted worldwide attention.

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Aspects of Costa Rica's diverse and complex tropical ecosystems are discussed by other contributors to this volume. Thus, we will not dwell further on this subject; rather, we will address the link between conservation and socioeconomic development in Costa Rica.

COSTA RICA AS A MODEL FOR INTERNATIONAL CONSERVATION

Costa Rica, a democratic country no larger than West Virginia, has developed a conservation program unmatched in the tropical world. Thanks to the initiative of a small group of bright young biologists, a comprehensive National Park System has been developed in less than 15 years, preserving nearly 10.27% of the country's land area, or about 524,917 hectares (Boza 1986). The park system is based on a clear objective of preserving representative tracts of the major life zones described by Holdridge et al. (1971). There are 23 parks and biological reserves (Boza 1986) (Fig. 1) and many of them, like Corcovado, Tortuguero, Santa Rosa, Amistad, and more recently Braulio Carrillo, are internationally recognized for their importance to species conservation.

We estimate that we are already protecting most of the best remaining examples of the country's twelve life zones. However, we must continue our effort to identify undisturbed areas in need of protection.

How has a poor country like Costa Rica been able to achieve this? Preserving such an extensive area of the country represents an investment of tens of millions of dollars at a time when the modest public treasury of the country has been severely affected by the global recession, and the nation is immersed in an ever-worsening debt crisis.

Costa Rica, which had the dubious honor of being the poorest province in the whole Spanish empire, developed in little over four centuries a standard of living unique for Latin America. Its geographical isolation, the scarcity of economic resources, and the misery of the colonial population shaped the character of our ancestors and established the solid basis of Costa Rican democracy. Our country historically lacked the striking socioeconomic differences between an aristocratic and wealthy ruling class and a subjugated poor and illiterate Indian population, which typified other Latin American societies. According to available statistics on current nutrition and life expectancy rates, the level of Costa Rican health is that of many industrialized nations (Hartshorn et al. 1982). This can be considered a clear indication that good health is more dependent on social policies than on the level of economic development. The benefits from education, justice and respect for human rights, environmental sanitation, standard of living, preventive medicine, and social security are of far greater magnitude in Costa Rica than in other Central American countries. The literacy rate of 91% is one of the highest in

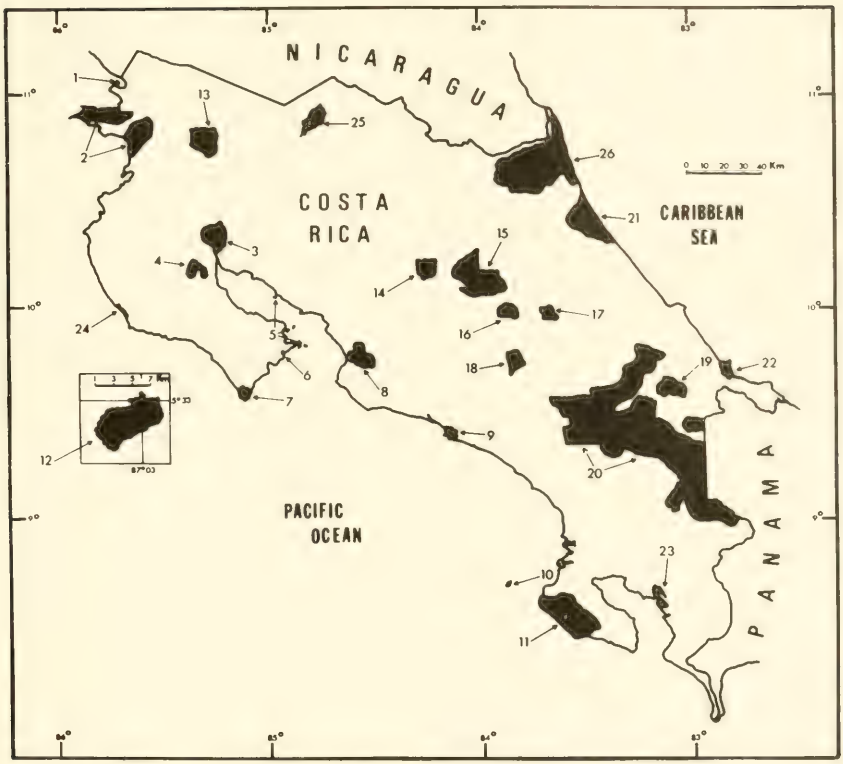

Fig. 1. Location of national parks and equivalent reserves in Costa Rica. 1. Refugio Nacional de Fauna Silvestre Isla Bolaños; 2. Parque Nacional Santa Rosa; 3. Parque Nacional Palo Verde y Refugio Nacional de Fauna Silvestre Dr. Rafael Lucas Rodríguez Caballero; 4. Parque Nacional Barra Honda; 5. Reservas Biológicas de las Islas Guayabo, Negritos y de Los Pájaros; 6. Refugio Nacional de Vida Silvestre Curú; 7. Reserva Natural Absoluta Cabo Blanco; 8. Reserva Biológica Carara; 9. Parque Nacional Manuel Antonio; 10. Reserva Biológica Isla del Caño; 11. Parque Nacional Corcovado; 12. Parque Nacional Isla del Coco; 13. Parque Nacional Rincón de la Vieja; 14. Parque Nacional Volcán Poás; 15. Parque Nacional Braulio Carrillo; 16. Parque Nacional Volcán Irazú; 17. Monumento Nacional Guayabo; 18. Refugio Nacional de Fauna Silvestre Tapantí; 19. Reserva Biológica Hitoy-Cerere; 20. Parque Nacional Chirripó y Parque Internacional la Amistad Costa Rica-Panamá; 21. Parque Nacional Tortuguero; 22. Parque Nacional Cahuita; 23. Refugio Nacional de Fauna Silvestre Golfito; 24. Refugio Nacional de Fauna Silvestre Ostional; 25. Refugio Nacional de Vida Silvestre Caño Negro; 26. Refugio Nacional de Fauna Silvestre Barra del Colorado. Modified from Boza 1986.

the hemisphere (Beebe 1984). What is more, Costa Rica, never a militaristic country, has officially had no army since 1949, showing the world that a political system based on peaceful coexistence is perfectly viable.

Conservation is congruent with the political and social values of the country. This is demonstrated by the increasing public and private support of conservation efforts, like the consolidation of our National Parks Foundation and other private agencies with similar objectives. International conservationist and philanthropic organizations, mostly from the United States, have provided over 5 million dollars and have cooperated in other ways to help us attain our goals. The campaign for the "Zona Protectora" (see Pringle, this volume), and its inclusion within the Braulio Carrillo National Park, is an example of increasing national and international awareness and comprehension of the importance of preserving irreplaceable tropical ecosystems. This transect is particularly valuable not only because of its biological wealth, but also because of its importance in tropical research and education and its proximity to the central metropolitan area of San José. We must not forget that this area is only a part of our vast network of parks and reserves, some of them, like Corcovado, facing more serious threats of destruction.

In Costa Rica there has been sympathetic acceptance of the foreign visitor, whether tourist, scientist or naturalist, who is attracted by the beauty and richness of our flora and fauna. The country has become an international center for research and training in tropical biology, even though the direct participation of Costa Ricans in these studies, while significant, has been modest. This is exemplified by the accomplishments of the Organization for Tropical Studies (see Stone, this volume) and the published literature based largely on research centered in Costa Rica (Clark 1985). It can be argued that Costa Rica, with its natural resources and traditional values supported by international academic and conservation organizations, has established a model system for the preservation of tropical diversity.

HOW VIABLE IS THIS MODEL?

However, Costa Rica's success must be set in a more global perspective; it cannot be taken out of context of the socioeconomic development pattern of the country and the use of its natural resources. We have to be realistic or our success may be seriously impaired.

Concurrently with its success in the area of conservation, Costa Rica has the dubious distinction of being the Latin American leader in the destruction of its natural resources. Hartshorn (pers. comm.) estimates that the deforestation rate in Costa Rica is the highest in Latin America; the country is losing its remaining forests at the rate of 3.66% per year, nine

times faster than Brazil, a country often cited for its relentless destruction of tropical forests. Brazil, of course, with its larger surface area, is losing more total forest.

According to the latest study of our Forest Service, Costa Rica's forests constitute the country's principal natural resource; two-thirds of the country is good only for forestry. But the country has destroyed nearly 60% of its forests to make way for agricultural pursuits or cattle ranching. Deforestation maps graphically demonstrate the startling change in the country's landscape over the past 43 years (see Fig. 2). The Tropical Science Center's country environmental profile (Hartshorn et al. 1982) discloses the magnitude of environmental deterioration. The conversion to pasture or agriculture of low-fertility soils on steep topography in areas of high rainfall is causing serious erosion and poor productivity. National estimates of pluvial erosion suggest that 17% of the country is already severely eroded. A rough estimate of soil loss comes to 680 million tons a year, of which 80% is caused by overgrazed pasture land (Hartshorn et al. 1982). But soil degradation is not limited to erosion losses; physical compaction, repeated burning, poor road design and construction, chemical toxification and inappropriate land use are also contributing to the deterioration of our soils. Since topsoil is essentially a non-renewable resource, the soil loss seriously threatens not only the country's productivity, but the economic viability of essential hydroelectric, irrigation, and forestry projects, and the availability of fresh water.

The rapid expansion of the metropolitan area of the Central Valley is eliminating some of the country's best agricultural lands and soils. The majority of Costa Rica's estimated population of 2.6 million live in the Central Valley. The population growth rate is approximately 2.2%. By the year 2000 the population of Costa Rica will be 3.4 million (Hartshorn et al. 1982). The country's major demographic problem is not simply a matter of frightening population growth, but rather how that population growth will relate to land availability, utilization, and tenure. Present population density in relation to available arable land is 225/km^2. This will reach approximately 384 km^2 by the end of the century, a figure not too different from those of tropical countries such as India or Bangladesh, or developed countries like Holland or Belgium (Hartshorn et al. 1982). The best land in our nation is close to saturation levels. These projections for the year 2000 and beyond must be taken seriously, if agriculture is to remain the basis of the country's socioeconomic development.

Agriculture has traditionally played a key role in Costa Rica's socioeconomic development, and is naturally expected to make even more substantial contributions to the solution of the current economic crisis. Agriculture accounts for approximately 28% of national employment, 19% of the GNP and 74% of export income (Hartshorn et al. 1982). The major exports

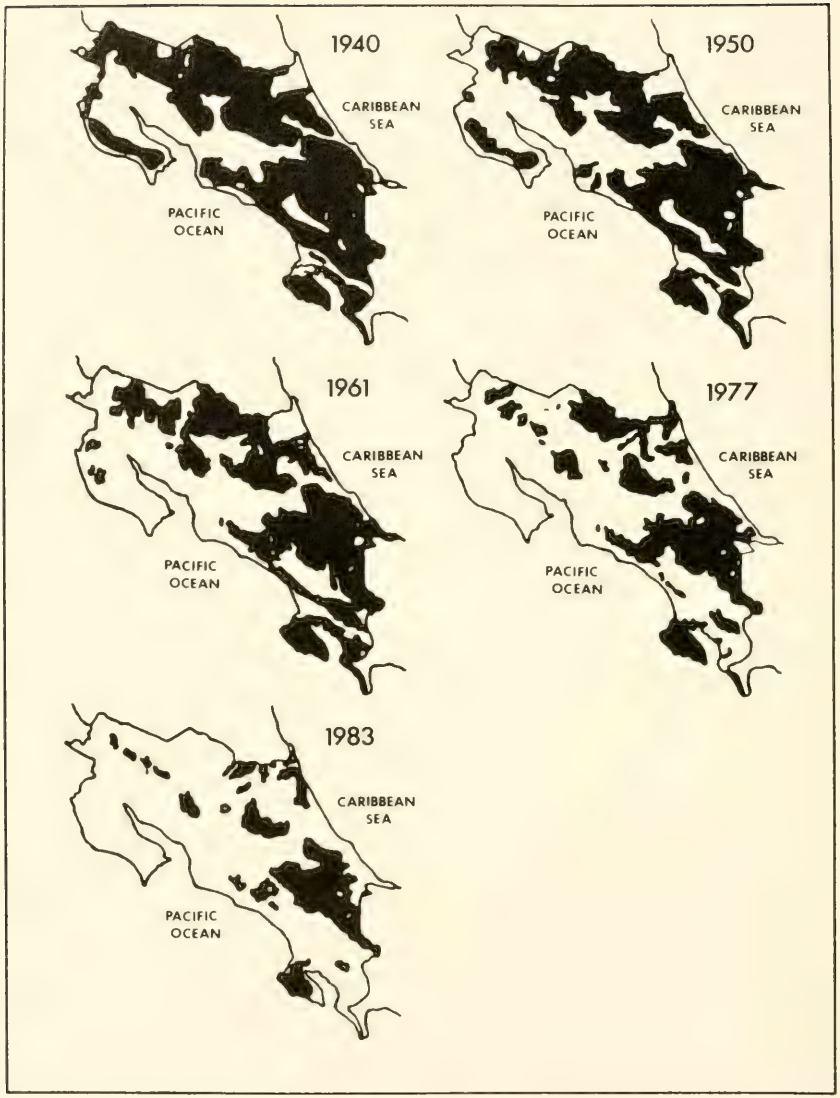

Fig. 2. Dense forest cover (80-100% of ground cover) in Costa Rica in 1940, 1950. 1961, 1977, and 1983. From Oficina de Planificación Sectorial Agrícola, Dirección General Forestal, Ministerio de Agricultura y Ganadería, Costa Rica.

are coffee, bananas, beef, and sugar, the traditional export commodities of developing countries in Central America, which frequently create a glut on international markets.

Beef cattle production has increased dramatically over the past two decades, as reflected by the dominant position of pasture land among farm uses (Hartshorn et al. 1982). Production efficiency for family size farms (20-200 ha) and large farms (over 200 ha) is very low, merely 122-162 kg/ha/year. A traditional predilection for beef cattle ranching is reflected in a willingness to sacrifice income to continue as a cattle rancher. Raising beef cattle also attracts urban investors who become absentee land owners or gentlemen farmers.

This is not intended to be a comprehensive analysis of the socioeconomic situation of Costa Rica and the inevitable effect on parks and environmental protection efforts. The country environmental profile (Hartshorn et al. 1982) summarizes the present socioeconomic situation as follows: "Costa Rica has a well-deserved, worldwide recognition for its stable democracy, rapid decline in population growth rate and exemplary system of national parks. Nevertheless, the country faces increasing pressures on natural resources along with concomitant environmental deterioration. The current economic crisis, the most severe in the country's history, will have profound and possibly unpredictable consequences on our natural resources and environmental conservation. Increased agricultural productivity and exports are expected to lead the country out of the economic morass, yet the best agricultural lands are being degraded by pervasive soil erosion or eliminated by sprawling urbanization. Extensive deforestation has nearly destroyed any potential for large-scale commercial forestry, while threatening the economic viability of hydroelectric, potable water, and irrigation projects."

Some parks already face other types of threats and pressures. For example, gold panners are digging up stream beds in Corcovado National Park and are causing profound damage to the rich ecosystems of the park (see Janzen et al. 1985). The abandonment of extensive banana plantations in adjacent parts of the Golfo Dulce region resulted in significant unemployment in the area and has contributed to the flood of gold panners in Corcovado. This has immersed Costa Rica's Osa Peninsula into a critical and complex social and economic situation that must be properly studied and resolved if Corcovado is to survive.

THE NEED FOR CHANGE AND ACTION

The effects of mismanaging natural environments in Costa Rica are already evident although not fully appreciated by all citizens and politicians. Nevertheless, some government planners and a new generation of politicians

and congressmen are starting to realize how expensive short-term profits can be in the long run. This perception fits into the country's overall concept of a new model for socioeconomic development that is sorely needed.

In order to reach the goal of making Costa Rica a developed country by the beginning of the next century, we must utilize all of our human, natural, and capital resources in an intelligent manner. At the same time, we must take advantage of our rich socioeconomic experience to broaden and deepen the very basis of our democratic lifestyle. In the past, we have imported luxury items and implicitly accepted the idea that development is to imitate the consumption patterns of highly developed countries. Clearly this must end. The country needs a lifestyle and a development strategy based on more work and greater austerity. Rational use of its natural resources is needed for a more humanized and egalitarian development. Emphasis on intensive rather than extensive agriculture would help meet the needs of the less privileged sectors of our population, including the large squatter population.

Economists and politicians are beginning to understand that conservation is not a romantic attitude reserved only for academia. In Costa Rica, some crude and startling preliminary figures are helping to change attitudes. According to the Forest Service, only 35% of the country's original forest cover remained in 1985. At the current rate of deforestation, some 150,000 acres (60,000 ha/yr) of forest, all in unmanaged areas, will be gone in less than five years; in about ten years only the national parks and some other equivalent areas will preserve forest ecosystems. Tragically, more than half of the timber cut, some 12 million m^3 (Dirección General Forestal 1985) a year is burned or allowed to rot *in situ* before cattle raising or some other form of subsistence agriculture takes over the land. It must be rather sobering for any economist or politician to know that if our commercial forests had been properly managed and preserved, they would be producing at least $3,500 million annually in different wood products, or 50% more than our 1982 GNP, as well as employing over 150,000 Costa Ricans in rural areas (Dirección General Forestal 1985). These figures represent only primary forestry industry, and do not take into account the added value of manufactured export products. Geographic location as well as existing infrastructure in the country are factors that could have made Costa Rica extremely competitive in the international market.

Unfortunately this tremendous potential, which represented perhaps the best option for the long-term development of our country, was not understood. Costa Rica has destroyed or seriously degraded over 60% of its original productive forest. Very little has been done to restore the forest cover. Little more than 5,000 ha have been reforested, according to recent estimates (Dirección General Forestal 1985). This will affect the lumber industry directly. Firewood, the main fuel for low-income families in rural areas,

provides over a third of the energy consumed by the country (Dirección General Forestal 1985).

The lumber industry is already facing grave problems. The raw lumber needed to maintain the existing timber industry at present levels would require annual importation of 3.3 million m^3, at an estimated price of $165 million (Dirección General Forestal 1985). However, very few countries will export their raw lumber. If our local lumber industry is closed down due to lack of raw material, the country will need to import nearly $500 million of lumber annually during the first 20 years of the next century. This is a substantially larger amount than we are presently paying for imported oil (Dirección General Forestal 1985). The option of sacrificing our remaining forest resources in the national parks and other protected areas is merely a stopgap measure that would accelerate ecological deterioration of the country.

On the other hand, our economists and politicians are beginning to realize that the floods, landslides, and drought triggered by deforestation are detrimental to the development of sound agricultural programs. Moreover, our leaders now realize that our national parks and reserves are now attracting nature tourism. The extraordinary biological diversity and scenic beauty of our mountains, rivers, and beaches attract more dollars than traditional activities such as cattle farming, which only lead to rapid, irreversible deforestation. Janzen (see Kaizer 1985) has recently stated that "establishing national parks is an economic alternative to traditional forest exploitation. If Costa Rica properly uses its resources to attract nature tourists and biologists, it could become the major location for tropical biology in the Western Hemisphere." Fortunately, this is already happening in Costa Rica; tourist agencies are promoting nature tours and Congress has recently passed new legislation promoting tourism. The Organization for Tropical Studies and similar independent scientific organizations and individuals are making Costa Rica a major research center in tropical biology.

The stewardship and protection of a national system of parks and reserves is a major effort that has not received the priority it truly deserves. The need for administrators and naturalists to staff the many parks, as well as the need for essential operating expenses, represent critical issues that organizations like our National Parks Foundation, local private organizations, and our North American counterparts are trying to address. The government should create one centralized agency at the highest administrative level in charge of the overall protection and management of its natural resources. We are already moving (albeit slowly) in this direction.

It is becoming clear that the country as a whole requires a new model for development that will satisfy its socioeconomic needs in harmony with its natural resources. Education is undoubtedly going to play a major role in this new concept of development. Conservation is something that concerns all

Costa Ricans. The concept that man is an integral part of nature has to become part of our national conscience.

In 1973 Janzen stated that tropical agroecosystems were misunderstood in the temperate zones and badly mismanaged in the tropics. This situation has not changed. The need for a new model for agricultural development is even more pressing today. There is an immediate need for more plantations of commercial timber and fuel wood to relieve pressure on undisturbed forests, national parks, and reserves. Agricultural advances should enable farmers to undertake intensive, stable cultivation rather than extensive, migratory cultivation. A system of "sustained-yield tropical agroecosystems" should serve as a guide for our agricultural research endeavors (see Gliessman, this volume).

Unfortunately we face a critical problem in the search for badly needed solutions. Largely because of the economic crisis, our country lacks the necessary funds and frequently the knowledge to implement many of these measures. Developed nations must acknowledge their stake in worldwide conservation. It is beyond the scope of this paper to analyze the framework of the political and economic relationships between rich and poor countries. Nevertheless it is a fact that we all form part of a socioeconomic web, and that to a certain extent, the destruction of our tropical forests has been determined by external economic pressures. Political leaders and intellectuals have stated in both the past and the present that temperate-zone countries have harvested tropical resources at prices quite unrelated to the real value of these resources in their places of origin. Social aspirations and consumption models frequently based on those of industrialized countries are totally irrelevant to the real needs and potentials of tropical countries.

The main point is that in the final analysis, the preservation of tropical biological diversity is a concern and responsibility that transcends political borders. Our efforts in Costa Rica cannot succeed without help from our friends in developed countries. It is very evident to us that the preservation of our exemplary national park system and our extraordinary biological diversity cannot and must not be seen as unrelated to the socioeconomic development of our country. Unlike most developing countries in Latin America, and other parts of the world, Costa Rica has implemented attitudinal changes within its social and political systems. We have the opportunity to create a model for the rational use of natural resources that can serve as an example for the rest of the world's tropical regions. We cannot afford to fail in this effort.

In order to meet the challenges of conservation and socioeconomic development, we have recently established (in addition to our well-known National Parks Foundation) a new foundation of broader scope, Neotropica, to tackle long-range and more pressing issues. A permanent center for the

study of environmental issues will play a fundamental role in the activities of the organization. This center will be guided by a core group of scientists, intellectuals, and other individuals concerned with the conservation and management of our natural resources. Typical issues addressed by Neotropica will include those dealing with:

(1) the legal conservation network
(2) the natural areas program and wildlife management
(3) environmental education and research
(4) the state of the environment
(5) watershed management
(6) marine resources
(7) management of forest resources
(8) ecotourism
(9) energy
(10) soils and land use.

We are well aware that policy decisions in these focal areas must be implemented as soon as possible. We must work in the areas of consensus, and progress gradually towards those of greater conflict and controversy.

As Costa Ricans we must move towards a socioeconomic and political model of development centered on a quality of life that would be viable and permanent only if it is based on a logical and rational use of our natural resources.

As a country and a society, Costa Rica has been successful in many ways, and we can hold up the creation and institutionalization of our national park system as an outstanding example. As Walt Whitman said: "...now understand me well—it is provided in the essence of things that from any fruition of success, no matter what, shall come forth something to make a greater struggle necessary."

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ADDENDUM

After this paper was submitted for publication, in February, 1986, the Costa Rican government evicted the gold panners from Corcovado National Park. Such action was promoted by massive national and international support from individuals and organizations concerned with the preservation of Corcovado. The search for a solution to the socioeconomic problems of the gold panners and the Osa Pensinsula is currently under way.

New legislation approved in March, 1986, imposes strict controls and penalties on deforestation or unauthorized logging, a measure expected to reduce substantially deforestation rates in the country.

In May, 1986, a bill to create the Ministry of Natural Resources, Energy, and Mining, to be in charge of the overall protection and management of natural resources, was submitted to Congress by the government of Costa Rica.

A presidential decree including "La Zona Protectora" within the Braulio Carrillo National Park was signed at La Selva in March, 1986.

THE ORGANIZATION FOR TROPICAL STUDIES (OTS): A SUCCESS STORY IN GRADUATE TRAINING AND RESEARCH

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The seeds for a cooperative program in tropical studies date back to the late 1950s. This common base of interest leading to the establishment of the Association for Tropical Biology in 1962 and the Organization for Tropical Studies in 1963 is documented, and the history and development of OTS is covered through the administration of five executive directors. The research and particularly the education programs that account for OTS's preeminence in tropical biology are surveyed. The last section on OTS TODAY presents an overview of current programs and alludes to new challenges and action plans that are designed to continue the success achieved in the first 23 years.

The Organization for Tropical Studies, Inc., familiarly known as OTS, is a highly successful consortium of universities and research institutions that has been primarily responsible for the United States' literacy in tropical biology. This symposium presents a fine opportunity to reexamine the development of OTS (Hubbell 1967; Harmon 1970) and the basis for its success in anticipation of the 25th anniversary in 1988.

A few words about the design of the paper are in order because it is divided into five sections of unequal length and emphasis. Section I, entitled PRE-OTS, examines the events in the U.S. scientific community that coalesced widespread interests in tropical biology and catalyzed action leading to OTS as well as the Association for Tropical Biology. Section II, ADMINISTRATIVE HISTORY OF OTS, constitutes the bulk of the profile that has involved a "cast of thousands" over the years. Although it is not possible to detail the roles of all those involved in OTS, individuals whose association with OTS has been long and noteworthy are highlighted. Section III, on EDUCATION, and section IV, on RESEARCH, are abbreviated renditions of

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the core programs whereby OTS has been successful and has made its most visible and lasting contributions to society. Many of the stories left untold here have to do with personal interactions and achievements of the thousands of students, faculty and researchers who have been influenced by their participation in OTS programs. Yet to come also is an objective evaluation of the impact that education and research programs have had on the national and international scene. Section V, OTS TODAY, carries events through the summer of 1986 and provides a thumbnail sketch of the consortium's aspirations for the future.

PRE-OTS

Independent Efforts in Tropical Studies

To understand why OTS has been successful in tropical education and research requires some knowledge of the roots from which the organization derives its strength (Table 1). The official birth of OTS was February 27, 1963, at the State Courthouse, Tallahassee, Florida. While this date marks the formal incorporation of the seven founding universities–Costa Rica, Florida, Harvard, Miami, Michigan, Southern California, and Washington–the seeds for a cooperative program in tropical studies date back to the late 1950s. Harvard was forced to cancel training and research programs at the Atkins Garden and Research Laboratory in Cuba with Castro's takeover in 1959, and Michigan had become frustrated in trying to establish a training center in southern Mexico. Michigan's efforts to develop a coordinated program in tropical studies started in 1957 when Theodore H. Hubbell was appointed to chair a Committee on a Proposed Center for Tropical Studies (Anon. 1965a). A plan was quickly drafted to establish a center in Chiapas, and by July 1958 a proposal was submitted to the U. S. National Science Foundation (NSF) and the Ford Foundation. Over the next several years the committee members made many trips to Mexico to arrange allocation of land for field sites with local, state and federal authorities, and details were worked out for curricula, logistics, and facilities (Anon. 1959). Tentative arrangements were made with the Universidad Nacional Autónoma de México, but firm agreements with Mexican authorities could not be reached and the idea of establishing a tropical center in Mexico was finally dropped in the spring of 1962. During this same period the Associated Colleges of the Midwest drew up a plan to establish an undergraduate, junior-year-abroad program in Costa Rica. The universities of Florida, Kansas and Miami all offered field biology courses in Latin America, and, in fact, Miami had opened negotiations with the Costa Rican government to acquire land for biological field stations (Hartweg 1963a). The University of Washington was added to the prospective fold because of its desire to find a tropical base for the forestry program.

TABLE 1. HISTORICAL EVENTS LEADING TO OTS INCORPORATION

Independent Efforts in Tropical Studies

Atkins Garden and Research Laboratory in Cuba used by Harvard University: forced out by Castro's takeover in 1959

University of Michigan attempts to establish center in Chiapas, Mexico: efforts initiated in 1957 and abandoned in 1962 for want of firm agreement with Mexican government

Associated Colleges of the Midwest, University of Florida, University of Kansas, and University of Miami all had field biology programs in Latin America in the late 1950s and early 1960s

National Science Foundation-sponsored Conferences & Programs

Miami, Florida, May 5-7, 1960: Conference on Tropical Botany

Fundamentals of Tropical Biology course in Costa Rica, 1961-1963, offered by the University of Southern California in conjunction with the University of Costa Rica

Costa Rica, April 23-27, 1962: Conference on Problems in Education and Research in Tropical Biology

Hodge & Keck Report, 1962: Biological Research Centers in Tropical America

Trinidad, July 2-6, 1962: Neotropical Botany Conference and founding of the Association for Tropical Biology

Jamaica, Dec. 17-21, 1962: meeting of representatives from Costa Rica Conference and Trinidad Conference

Formation of OTS

Coral Gables, Florida, Jan. 31-Feb. 2, 1963: meeting of Organizing Committee

State of Florida, Feb. 27, 1963: incorporation

Miami, Florida, June 25-26, 1963: first formal Board meeting

San José, Costa Rica, Nov. 8-11, 1963: first annual Board meeting

Miami Conference of 1960

The ferment of interest in tropical biology prompted NSF to examine the status of teaching and research on tropical plants, and on discovering that little information was available, a Conference on Tropical Botany was called at the Fairchild Tropical Garden in Miami, Florida on May 5-7, 1960. The Miami Conference was seminal in the development of a national awareness of the tropics, and the general conclusions that were drawn established the tone and framework for subsequent scientific efforts in training and research (NRC 1960). The conference concluded with the following recommendations:

"Tropical botany is now and will become increasingly important as an area demanding maximum cooperation between men of all nations concerned, because of man's dependence on the plants of his environment, the continuing and rapid growth of populations and the associated depletion of natural vegetation regions and resources.

"Field botanical research on tropical vegetation should be greatly augmented in the immediate future because the destruction of natural vegetation places a limit on the time available for the study of undisturbed tropical vegetation.

"The location and identification of tropical plants as resources for basic scientific study, for use in industry and medicine, for ornamental and agricultural horticulture, and the support of investigations and the training of students will benefit the country of origin and the country of utilization.

"Field stations in the tropics and subtropics are extremely important for botanical teaching and research. Existing field stations should be utilized to the fullest extent, and new field stations should be planned and supported according to demonstrated need.

"Practical taxonomic information is a recognized need for almost all botanical research, and local floras including all groups of plants should be prepared for tropical regions where botanical studies are conducted. At the same time, active support should be given to implement a coordinated program of monographs on tropical American plants.

"Existing textbooks of botany are based largely on conditions and plants of the temperate regions. The preparation of texts which encompass the tropics should be encouraged.

"While it is recognized that taxonomy is basic, plant geography, ecology with its application to land use, plant pathology, plant physiology, economic botany, anatomy, genetics, cytology, morphology, and other botanical disciplines have important roles in the development of knowledge of tropical botany."

Fundamentals of Tropical Biology Course

One of the first and most visible moves to address the deficiency in U.S. scientists trained in tropical biology came in 1961. The University of Southern California (USC), with the helping hand of James S. Bethel in Science Education at NSF (J. M. Savage, pers. comm.), received NSF and Organization of American States funding to teach Biology 505L, Fundamentals of Tropical Biology, in Costa Rica. This course, under the direction of Jay M. Savage and with the cooperation of faculty from the University of Costa Rica (UCR), was designed to provide "college and university teachers with a basic understanding of biological phenomena in the tropics through firsthand study in tropical environments" (Savage 1961). One can imagine

the excitement of the 15 U.S. and five Latin American participants. Here was a unique opportunity for educators to see firsthand what they had been lecturing about for years. This first course had the traditional classroom lectures and accompanying laboratories, and seven field trips exposed the participants to soaring volcanic peaks, treeless páramos, deciduous dry forests, and lush tropical lowland rainforests. The Fundamentals course was repeated under USC and UCR sponsorship in 1962 and 1963, and additional opportunities were afforded to a select group of college professors for short periods of full-time research (Savage 1963a). In the summer of 1963, twelve graduate students were added to the mix to determine if the program could serve equally well for the novice college professor and the young graduate. Among this set of participants was a UC Berkeley student by the name of Daniel H. Janzen, who subsequently went on to put his own stamp of genius on the OTS training programs.

Costa Rica Conference of 1962

The first course showed the way for introducing tropical biology to an eager community of U.S. scientists. In the spring of 1962 Savage, Rafael Lucas Rodríguez, and J. Robert Hunter, under the auspices of NSF, organized a key Conference on Problems in Education and Research in Tropical Biology. This conference was held in San José, Costa Rica on April 23-27 to consider: (1) the minimal basic requirements for education and research in tropical biology; (2) how existing demands for education and research, facilities and trained tropical biologists could be met; and (3) a program for coordinating the many individual projects in education and research in tropical biology (Savage 1962).

The five-day session was intense. The first two days were designed to orient the 31 participants to the tropics, to Costa Rica and to the purpose and format of the conference (R. L. Rodríguez); to summarize the present state of tropical biology (J. R. Hunter); and to outline an experimental program of education in tropical biology (J. M. Savage). These formal presentations were followed by panel discussions involving Costa Rican residents John DeAbate, Lester R. Holdridge, Alfonso Jiménez, and Joseph A. Tosi, Jr. The third day was devoted to field trips to survey sites for the education and research programs. The participants split into three groups: one going to a marine site near Mata Limón on the Pacific Coast; one to view Carlos Lankester's orchid garden in Cartago and vegetational associations along a 4,000-9,500 ft. elevational transect on Volcán Irazú; and the third to tour the Instituto Interamericano Ciencias Agrícolas (IICA) facilities at Turrialba. The background provided by the first three days of the conference and the expertise of invited participants were drawn on in the fourth day at the

"small conference sessions." Reports from these groups laid the cornerstones for OTS by developing the rationale and plan of action for meeting critical needs of teaching and research in tropical biology (Savage 1962). The four sets of recommendations that follow covered programs and facilities needed to engage in tropical education and research.

(1) Undergraduate, graduate, and postdoctoral education, chaired by Cornelius H. Muller, recommended: (a) the recruitment of undergraduates early in their careers so that a commitment to the tropics is inculcated; (b) a program of basic education in tropical biology for students at the graduate level; (c) a similar program for postdoctoral biologists without tropical experience; and (d) a coordinated effort to encourage and develop research as the base for graduate thesis preparation and recruitment of postdoctoral scientists into tropical research.

(2) Crucial problems in tropical research, chaired by Damon Boynton, identified seven broad areas of research priorities: (a) flora, fauna, and ecological associations, both recent and fossil, under tropical conditions; (b) biogeography and evolutionary biology including cytogenetics and allied subjects; (c) population and community dynamics, including man, under tropical conditions; (d) tropical climates, microclimates, and soils; (e) methodology for the determination of natural resources and the conservation thereof; (f) physiological and biochemical response of tropical plants and animals to variations in the environmental complex; and (g) geological features and processes pertaining to tropical biology.

(3) Facilities requirements for education, chaired by I. Duncan Clement, concluded that any proposed center must be a cooperative project organized on a hemispheric basis with headquarters in Costa Rica, but committed to developing facilities in other Latin American areas in the future. Minimal education needs include: (a) a basic central building with at least a dirty or wet laboratory and a clean teaching laboratory; (b) a working collection of local biota; (c) a working office laboratory and library; (d) a simple woodworking and metalworking shop; (e) adequate teaching equipment, especially projectors and screen, compound and dissecting microscopes and field glasses; (f) minimal field and collecting gear; (g) field vehicles; (h) adjacent animal quarters and plant-growing areas for simple behavioral and experimental studies; (i) simple field stations and permanent sites for study and observation; (j) adequate housing for staff and students; and (k) a permanent staff under the direction of a resident professional tropical biologist.

(4) Facilities requirements for research, chaired by E. Peter Volpe, recognized the ideal as a "multi-million dollar installation, involving the establishment of a centralized edifice and permanent field stations in select areas of Costa Rica." As minimal requirements the group listed the needs in three categories: (a) natural—areas with original, natural, or undisturbed

habitats; (b) human—permanent staff of knowledgeable individuals who can provide intimate knowledge of various aspects of Costa Rica; and (c) physical —field vehicles and laboratories equipped with microscopes, balances, photographic equipment, herbaria, stockrooms, etc.

The session concluded on the fifth day with the resolve to establish permanent headquarters in San José, Costa Rica and to act immediately on implementing recommendations for programs and facilities to further education and research in tropical biology. The participants voted to constitute themselves as a permanent body devoted to implementing the action plan of the small conference sessions. An executive committee was formed from the six members of the Conference Steering Committee (viz. J. DeAbate, L. R. Holdridge, J. R. Hunter, A. Jiménez, R. L. Rodríguez and J. M. Savage) and seven persons were elected from the delegates at large: F. S. Barkalow, Jr., I. D. Clement, N. E. Hartweg, W. H. Leigh, G. Mann, C. H. Muller, and F. W. Went. Hunter was subsequently elected chairman and Clement and Went were appointed as official representatives to meet with participants of the forthcoming Neotropical Botany Conference in Trinidad.

Hodge and Keck Report

Concurrent with the USC/UCR training program, NSF conducted its own field survey of the Biological Research Centers in Tropical America. In light of the 1960 Miami conference findings, Walter H. Hodge and David D. Keck (1962) set out to ascertain the sites where "basic biological research and/or research training may be conducted and where the participation of foreign scientists is invited." In their coverage of fifteen Latin American countries and six West Indian islands, Costa Rica and UCR in particular were identified as prime locations for tropical studies with the following complimentary remarks:

"The most up and coming University in Central America and one with a number of cooperative programs with U.S. institutions, and the site of two NSF summer training institutes. The new campus has modern buildings and facilities for most kinds of biological work carried out mainly in departments of botany, biology, entomology and microbiology. Because of its facilities—including an ample library, and the proximity of a wide variety of nearly [nearby?] natural areas, a fine plant collection (of C. Lankaster in Cartago), and potential branch field stations in the country—this University has been recommended as the site of a permanent center for indoctrinating United States scientists and their students in tropical Biology. The University is much interested in all such programs."

Trinidad Conference of 1962

The third in the series of conferences sponsored by NSF was held at the Imperial College of Tropical Agriculture, St. Augustine, Trinidad on July 2-6, 1962 (Purseglove 1962). The 37 or so participants at the Neotropical Botany Conference discussed the report of the Costa Rica Conference and then heard nine botanical specialists outline major gaps in botanical knowledge of the Neotropics: opening session, John W. Purseglove; taxonomy and collecting, Bassett Maguire; ecology and conservation, Stanley A. Cain; morphology and anatomy, William L. Stern; plant physiology, Kenneth V. Thimann; cytogenetics, F. W. Cope; cryptogamic botany, George R. Proctor; economic botany, Louis O. Williams; and evolution, Herbert G. Baker. Following an enumeration by A. C. Smith of the facilities available in the Neotropics for teaching and research in tropical biology (after Hodge and Keck 1962), the Trinidad Conference concluded on July 6 with a resolution to "bring into being" the Association for Tropical Biology (ATB) (Purseglove 1962:43). Mixed opinions existed as to the impact and relation this new society would have to the proposals fostered by the Costa Rica Conference, but the Executive Committee of the Association was authorized "to co-opt one or two delegates... to achieve a meeting of minds, action and participation" (Purseglove 1962:46). Furthermore, I. D. Clement was designated as the liaison to invite Costa Rica Conference participants to join the ATB.

Jamaica Meeting of 1962

The stage was set for a meeting of the two groups in Port Antonio, Jamaica on December 17-21, 1962. The mindset and expectations of the participants must have differed. To those from the Trinidad Conference, the ATB was viewed as "the central or parent organization to which others of more special interest" could become affiliated (Maguire 1966: 7,8). No doubt J. W. Purseglove, chairman, Tobias Lasser and B. Maguire conveyed this attitude when they met with J. DeAbate, J. R. Hunter and J. M. Savage from the Costa Rica Conference. In any case Purseglove reports that the Costa Rica Conference was dissolved and merged with the ATB (Purseglove 1964:2). Quite to the contrary, however, the two groups did not merge, and this meeting in Jamaica has to be regarded as the formal point of divergence. Savage's impression was that the wheels were already in motion for a Center or Organization for Tropical Studies (Savage, pers. commun.), and Purseglove's reference to merger applied to invitations extended to individual membership in ATB. Certainly this latter explanation is consistent with the events, for just prior to the Jamaica meetings a "Proposal for the Establishment of a Center for Tropical Studies" in Costa Rica was being circulated by the University of Michigan (Anon. 1962).

The Jamaica meeting marks the close of preliminary discussions leading to the formation of OTS. The botanical community has to be given credit for publicizing the problems and challenges of working in the tropics, in the course of reaching this point. All of the persons who attended two or more of the conferences were plant scientists. Fourteen participants were present at both the 1960 Miami Conference and the 1962 Trinidad Conference (Baker, Cain, Clement, Fosberg, Hodge, Keck, Howard, Maguire, Mathias, McVaugh, Purseglove, Smith, Went, and Williams), three individuals (Bethel, Holdridge, and Noggle) attended one of these meetings as well as the 1962 Costa Rica Conference, and two peripatetics (Clement and Went) were present at all three sessions (see NRC 1960, Savage 1962, Purseglove 1962). OTS stands solidly on these botanical foundations; however, the vitality of the consortium derived from the melting pot of scientists from the seven founding institutions.

Coral Gables Meeting of 1963

The formal steps to establish OTS were initiated by Norman E. Hartweg as Chairman of the Michigan CenTrop committee. On December 3, 1962, he wrote invitational letters to representatives of nine institutions to convene at the University of Miami in Coral Gables, Florida on January 31 - February 2, 1963 (Hartweg 1963b). This meeting touched on the high points leading to the proposal for establishment of the Organization for Tropical Studies and outlined the organization and facilities that would be needed to implement the educational programs. "It was there that the bullet was bitten and concrete steps taken" (Rollins 1986) to establish OTS by drawing up by-laws and submitting the charter to the State of Florida (Hartweg 1963a).

At the time of the Coral Gables meetings, several of the schools were uncertain about making a formal commitment to OTS membership and, in fact, the Associated Colleges of the Midwest and the New York Botanical Garden later declined membership. Many other potential members were never given the opportunity to make this choice because the invitations to attend were only sent to a subset of institutions that participated in the Costa Rica and/or the Jamaica conferences. The University of Kansas, for example, was not represented at this meeting, but because of intense interest it submitted a formal request for membership in the spring of 1963.

ADMINISTRATIVE HISTORY OF OTS

The Early Years of OTS

The first formal Board meeting was held in Miami on June 25-26, 1963 (Savage 1963b). At this time the University of Kansas was accepted as a

charter member[1], to bring the membership to eight, and a six-person Executive Committee was elected with N.E. Hartweg as President and Chairman; J. DeAbate, Vice President; J. M. Savage, Secretary; W. H. Leigh, Treasurer; and J. S. Bethel and Reed C. Rollins, Members at Large. By the OTS Charter of February 1, 1963 (Hartweg 1963a), and persisting to this day, "at least one director designated by a member institution shall be a scientist and not more than one director shall be an administrative officer of the member institution." The wisdom of this requirement is now self-evident, and it was such a group that charted the early course for OTS and developed some lofty expectations that have yet to be realized. For example, in the dealings with NSF regarding funding for educational programs and facilities in Costa Rica, there was an implicit understanding or expectation at least that OTS would be designated as a "national laboratory" comparable to the Kitt Peak National Observatory or the National Center for Atmospheric Research (Bethel 1965, Hubbell 1965a,b). Unfortunately this status and the stability provided through core financial support never materialized (Bethel 1966). In its place OTS relied on a small dues commitment from its members, a $2,500 initiation fee and $2,000 annual dues thereafter, and program funds provided by an ephemeral assortment of government and private granting agencies.

The personal commitment of the Board members and the great promise of OTS overcame many obstacles in the 1963-1964 period, but finances limited development of the organizational structure. J. M. Savage was hired on an interim basis as Executive Secretary and J. DeAbate as Special Consultant to mobilize the Fundamentals course for the summer of 1964 (Savage 1963c). The youthful organization received a major setback when President Hartweg died in February 1964 (Savage 1964d). R. C. Rollins was elected president by mail ballot to step into the breach during this crucial phase of funding negotiations with Science Education at NSF. Savage operated out of Costa Rica in the spring of 1964 in order to organize the summer OTS course, and both he and DeAbate worked to strengthen ties with local institutions and to develop new ones in other Latin countries (Savage 1964a). Conversations were initiated at this time with UCR officials about construction of OTS facilities, and an agreement was being sought with the government Institute of Land Colonization (ITCO) to establish field sites for education and research (Salazar 1964). Apparently ITCO wanted the sites to be extensive so that they could serve as the nucleus for a future National Park System (Savage 1964b).

OTS's need for a full-time director was appreciated from the beginning of Rollins' reluctant ascendency to presidency, and by July 1964, William

[1] The University of California was subsequently admitted on November 13, 1964 as the ninth and last charter member.

Hatheway, formerly with the Rockefeller Foundation in Mexico City, had been selected as the first Executive Director (Savage 1964c). With the University of Miami acting as fiscal agent at no cost to OTS, Hatheway moved to Costa Rica to head the operation. The departure of Savage prior to Hatheway's arrival in late September led to some communication problems regarding grant-writing responsibilities. Although the issues were satisfactorily resolved through President Rollins' coordination, it was a bad omen for the new Executive Director. Hatheway was, of course, plagued from the start by organizational work in anticipation of the two courses scheduled for the winter of 1965. Further, he was challenged by the perceptive comments of Charles D. Michener (1964) to orient the course away from the classroom and into the field. Hatheway proposed a revised curriculum that scaled back on short-term visiting faculty and lectures and placed greater emphasis on spending longer time at each field site with a few senior faculty. In particular, Hatheway felt so strongly that L. R. Holdridge's expertise in vegetation and tropical tree identification was indispensable to the Fundamentals course that Holdridge was proposed as the principal instructor, with Hatheway and D. H. Janzen serving as assistants (Hatheway 1964).

Holdridge's willingness to assume a major role in the 1965 winter Fundamentals course was predicated on his position as coordinator and a contract with OTS giving the Tropical Science Center (TSC) full authority to handle the course (Hatheway 1964). This latter proposal was reviewed with some skepticism by Rollins from the very beginning because he felt that under no circumstances could the fledgling OTS consortium afford to "become a satellite of the Tropical Science Center" (Rollins 1964a). Although this contractual arrangement was thought to have the tacit endorsement of UCR faculty such as R. L. Rodríguez, Rollins realized that dependence on TSC for course logistics and development would do nothing for building the OTS capabilities and would tend to weaken the involvement with UCR. Rollins (1964b) repeatedly warned Hatheway about forming too tight a link with TSC, but on January 5, 1965, a contract was signed with J. R. Hunter that gave TSC responsibility "for the entire conduct of the course including instruction, course materials, field trips, handling and accounting of funds and all other matters relating to this course" (Anon. 1965b).

Problems faced Hatheway from the beginning. The advertisements that were sent out for the winter courses attracted a lot of interest and applications, but the problems of foreign mail and the lack of timely communication with the course applicants created confusion and discontent (Michener 1965). The problems only magnified once the courses got under way. The Tropical Forest Ecology course led by Paul W. Richards was not covered by the contract, so this group avoided the sniping and friction that developed between Holdridge and some of his staff and students in the Fundamentals

course. Animosity was expressed over TSC's efforts to control all aspects of course activity, and particularly their insistence that the use of field sites and facilities in Costa Rica be cleared through them. Apparently TSC viewed OTS as a potential competitor and the paranoia extended to the development of "exclusive-use rights" contracts with companies and private land holders (Woodman 1965). The final straw came when UCR refused to process credits for the 1965 winter course on the grounds that TSC was not an academic institution (Janzen 1965).

Hatheway's inability to cope with the situation brought Rollins to San José for a confrontation on February 16-18. As a result of this meeting, Hatheway resigned (Hatheway 1965a) and returned with pleasure to field botany (Hatheway 1965b). At this point, President Rollins turned to DeAbate and Janzen for the organizational development of the 1965 summer course program, and at the March 21 meeting of the Executive Committee, Rollins' forceful action was endorsed and formal ties with TSC were severed (Savage 1965). This meeting brought the first OTS crises to a close and marked a turning point toward stability with the identification of Stephen B. Preston as interim Executive Director.

The Preston Era, 1965-1968

The summer of 1965 afforded a fresh start for OTS. The course programming was in the competent and energetic hands of D. H. Janzen, while J. DeAbate deftly cut the administrative red tape at UCR. Preston not only had the advantage of inheriting these two seasoned staffers, but he also benefited from the hindsight provided by W. H. Hatheway's trials and tribulations. In May of 1965, two months prior to assuming the OTS directorship, Preston had identified several "problem areas in OTS operation" in a special report requested by the Executive Committee (Preston 1965). One problem had to do with strained relations at UCR. Apparently DeAbate had been exceptionally aggressive and effective in negotiating for space and other privileges, and these efforts were resented by some faculty because he had dealt directly with the individual schools and departments, rather than channeling OTS requests through the upper echelon. The TSC brouhaha was recognized as an unfortunate event that left resentment on both sides. On the other hand, Preston was not ready to close out future options of establishing working relationships with TSC. Preston also surmised that the Costa Rican staff did not have a clear understanding of the thinking of the Executive Committee and had little knowledge of the activities of the member universities in relation to OTS, with the consequence that local operations were developed in a vacuum without institutional input. Preston concluded that the new executive director should spend a significant amount of time in the U.S. to

ensure liaison with the prime funding sources and majority of the consortium constituency.

The operational details proved time-consuming for Preston during his first year at the helm, and the hoped-for liaison with member institutions was limited. The time was ripe for the administrative restructuring proposed by T. H. Hubbell (1966) to strengthen and improve the organization. Among other things he recommended that the central office of OTS be moved from San José to the U.S. (Preston's home base at the University of Michigan), and that an assistant executive director be added to the staff to handle the operations of the San José office in the absence of the executive director. These recommendations were later adopted and to this day serve as the organizational framework for OTS.

Preston's interim directorship was stretched to three and one-half productive years, overlapping with the dynamic and forceful presidencies of J.S. Bethel and Stephen H. Spurr. During part of this period the University of Michigan provided Ross N. Pearson on release time to serve as Associate Director of Education, and the University of Washington assigned Dale W. Cole to handle duties of the Associate Director of Research. Jorge R. Campabadal was hired as an assistant during Preston's second year, but in a matter of months he proved his organizational skills and was elevated to Resident Director, a position he held for nearly 11 years that spanned the terms of six presidents (Table 2) and four executive directors (Table 3).

The late 1960s were a time of action and growth on all fronts (Argersinger 1967). Ford Foundation and NSF support between 1967-1970 funded over 90 pre- and postdoctoral pilot research projects. This was also a time when field sites were being sought for long-term training and research programs. Discussions were held with the United Fruit Company about use and possible management of the Lancetilla Botanical Garden in Tela, Honduras, and with Roberto (Bobby) Dorion, President of El Salto, S.A., about establishing a teaching and research center on the 10,000-acre sugar farm near Escuintla in western Guatemala. Preliminary consideration was even given to establish a Northern South American (Andean) OTS Center, and Thomas C. Emmel was sent on a reconnaissance (Teas 1969). A purchase option was taken in 1967 to buy La Selva from L. R. Holdridge, and arrangements were made with G. David Stewart of COMELCO ranch to lease space at Palo Verde for construction of a field station. As early as 1966 a multi-investigator research project was designed to compare the ecosystems of tropical lowland forest communities. When the proposal was submitted for funding to NSF in 1967, Palo Verde and La Selva were identified as the long-term study sites. This was also the period that the OTS emblem was designed under the guidance of Thomas E. Moore at the University of Michigan and formally adopted by the Board of Directors at the meeting of November 8, 1968.

TABLE 2. OTS PRESIDENTS 1963-1988

Tenure of President		Domain of Board Meetings
1963-1964	Norman E. Hartweg	June 25-26, 1963. Nov. 8-11, 1963.
1964-1965	Reed C. Rollins	Nov. 13, 1964. Nov. 12, 1965.
1965-1967	James S. Bethel	Nov. 11-12, 1966. Nov. 10-11, 1967.
1967-1968	Stephen H. Spurr	Nov. 7-9, 1968.
1968-1971	Mildred E. Mathias	Nov. 14-15, 1969. Nov. 13-14, 1970.
1971-1973	Joseph M. Reynolds	Nov. 11-13, 1971. Jan. 12-13, 1973.
1973-1974	Stephen B. Preston	Nov. 9-10, 1973. Nov. 8-9, 1974.
1974-1980	Jay M. Savage	Nov. 14-15, 1975. Nov. 12-13, 1976. Nov. 11-12, 1977. Nov. 10-11, 1978. Nov. 16-17, 1979. Apr. 12, 1980.
1980-1985	Thomas M. Yuill	Mar. 27-28, 1981. Mar. 19-20, 1982. Apr. 15-16, 1983. Mar. 23-24, 1984. Mar. 29-30, 1985.
1985-	Peter H. Raven	Mar. 21-22, 1986. Mar. 20-21, 1987.

The Spencer Era, 1968-1972

The protracted interim directorship of Preston came to a close with Jack T. Spencer's appointment-elect in October 1968. Spencer had been a former program officer at NSF and was thus familiar with the fledgling OTS programs. He was also aware of NSF's encouragement for OTS to establish a financial office (Teas 1969) in order to untangle the financial records being kept at Michigan and the University of Miami (Spencer 1986), and this became part of the transition in leadership when the North American Office (NAO) moved in December 1968 from Michigan to the Miami campus (Spencer 1969). Almost from the start, however, the limited free space that could be provided by the University was inadequate to house the expanding headquarters, and by the spring of 1970 NAO moved off campus and rented quarters in a nearby office building in South Miami.

The year 1969 stands as one of the most intense periods in the development of OTS infrastructure (Marts 1969): formal guidelines were drawn up for most OTS business and program activities; a provisional indirect cost rate (47%) was established with NSF; a five-year development plan was drafted; formal advisory committees were constituted for earth sciences, geography,

TABLE 3. OTS ADMINISTRATION 1963-1986

Administrator and Title	Term of Appointment
*Jay M. Savage, Executive Secretary	Sept. 1963-Aug. 1964
*John DeAbate, Special Consultant	Nov. 1963-Oct. 1964
Deputy Director	Nov. 1964-Mar. 1965
Acting Executive Director	Mar. 1965-June 1965
*William H. Hatheway, Executive Director	Sept. 1964-Apr. 1965
*Stephen B. Preston, Executive Director (NAO)	Jun. 1965- Dec. 1968
Norman J. Scott, Asst. to Director (CRO)	July 1966-Jan. 1967
Jorge R. Campabadal, Asst. to Director (CRO)	Mar. 1967-Nov. 1967
Resident Director (CRO)	Nov. 1967-Jan. 1978
Ross N. Pearson, Assoc. Director Education (NAO)	Sept. 1967-Aug. 1969
Dale W. Cole, Assoc. Director Research (NAO)	Spring 1968-Spr. 1970
*Jack T. Spencer, Executive Director (NAO)	Jan. 1969-June 1972
John P. Brand, Assoc. Director Education (NAO)	Sept. 1969-Aug. 1970
Benjamin H. Waite, Asst. Dir. Acad. Affairs (CRO)	Jan. 1971-Jan. 1973
*Kenneth J. Turnbull, Exec. Director (NAO)	July 1972-Feb. 1976
Robert G. Wilson, Sta. Director (Las Cruces)	Apr. 1973-June 1986
David P. Janos, Sta. Mgr. (La Selva)	Jan. 1975-Aug. 1975
Mario Baudoin, Sta. Mgr. (La Selva)	Nov. 1975-Aug. 1976
*Donald E. Stone, Interim Exec. Director (NAO)	Apr. 1976-Nov. 1976
Executive Director (NAO)	Nov. 1976-Present
James E. Crisp, Sta. Mgr. (La Selva)	Dec. 1976-Aug. 1977
Lucinda A. McDade, Sta. Mgr. (La Selva)	Sept. 1977-Feb. 1978
Scientific Coordinator (NAO)	June 1985-Present
Flor M. Torres A., Act. Asst. Resident Dir. (CRO)	Feb. 1978-Mar. 1978
Chief of Operations (CRO)	Mar. 1978-Dec. 1983
Robert L. Sanford, Jr., Sta. Mgr. (La Selva)	Apr. 1978-Aug. 1978
Thomas S. Ray, Jr., and Catherine C. Andrews, Sta. Co-Mgrs. (La Selva)	Aug. 1978-June 1979
Philip J. DeVries, Sta. Mgr. (La Selva)	July 1979-Dec. 1979
David B. Clark & Deborah A. Clark, Sta. Co-Directors (La Selva)	Jan. 1980-Present
Charles E. Schnell, Interim Chief of Oper. (CRO)	Dec. 1983-July 1984
Chief of Operations (CRO)	Aug. 1984-Dec. 1984
Resident Director (CRO)	Jan. 1985-Present
Luís Diego Gomez, Sta. Director (Las Cruces)	July 1986-Present

*Chief Executive Officer

marine science, meteorology, and terrestrial biology; and *ad hoc* committees were formed to consider Spanish language teaching, institutional membership, the North Andean Center, physical facilities, policy for station use, and ecosystem control. Fortunately this was a peak year for NSF support, and the future looked bright with a strong administrative staff and Mildred E. Mathias as the articulate, persuasive president, with needed leadership qualities (Marts 1969). In 1969 OTS had 25 institutional members (Spencer 1969), but a maximum of 17 enjoyed the rights of voting. The basis for this disfranchisement stemmed from the charter member's interest in regulating growth while ensuring their "full involvement" (Marts 1969). A three-tiered system was in place in which all institutional representatives were part of the Advisory Council. The Council in turn elected a 17-person Board of Directors, and from this group an 8-person Executive Committee was chosen. Discontent amongst the new memberships led Stephen H. Spurr to propose a re-evaluation of the Charter and By-Laws with the idea of combining the Advisory Council and Board of Directors. This action was taken, to the relief of many, at the next annual Board meeting (Marts 1970) and full voting rights were granted to all institutional representatives (Mathias 1986). On other fronts, two years of formal negotiations with El Salto, S.A., led to the signing of a contract (July 11, 1969) that provided OTS with a base of operation in Guatemala in exchange for a monthly payment of $100. Ten courses were scheduled for 1969, but the expenditure ceiling imposed by NSF trimmed the final offerings to seven. This ceiling also limited the NSF-funded Ecosystem Comparison study that got off the ground in mid-1968.

By 1970 OTS gave a peak number of nine courses. Operations of as many as five simultaneous field courses required masterful logistic planning by Resident Director Campabadal. Behind the scenes NSF was keeping close tabs on course structure, student body, and finances. Alice Withrow, program officer in the NSF Education Directorate, was a vigorous mother hen who "ruled the roost on the educational funding for OTS" (Spencer 1986). Stringent limitations were placed on the use of NSF funds for supporting foreign students, and Foundation involvement seemed excessive at times. Friction between Withrow and the OTS administration made life difficult, but even so the courses were establishing a reputation of excellence and "Doña Alice" was immortalized in the name of the OTS bus. This was also the time when the impressive collection of course handouts was deemed worthy of editorial synthesis and Charles E. Schnell, graduate student at Harvard University, was retained to assemble "The Book" of biological and environmental data about the OTS study sites in Costa Rica (Schnell 1971). The course programming made use of the Smithsonian Tropical Research Institute facilities in Panama, of Discovery Bay in Jamaica, San Andres Island, Colombia and of Finca El Salto in Guatemala. The moratorium placed on

institutional membership during all of 1969 was lifted, and membership grew to 27. Meanwhile the OTS staff had reached the robust number of seven in NAO and thirteen at the Costa Rican Office (CRO) (Spencer 1970). La Selva, which was acquired in 1968, was provided with funds by the Ecosystem Comparison study for a land survey and establishment of field facilities. Plans were on the drawing board in 1970 for a 20x40 ft. research laboratory, and a new concrete footbridge was completed to the Arboretum. Ground was broken on February 18 for a field station building at Palo Verde, and an agreement was established with Robert G. Wilson at Las Cruces to use the newly constructed Stanley Smith Science Building that was designed to fit OTS needs.

In spite of the obvious strengths of the education programs and the great potential of the comparative ecosystem research program, the OTS horizon was clouded by financial insecurity. The limited income from institutional dues was insufficient to cover the administrative costs, and heavy reliance was placed on indirect cost recovery from the NSF grants. The national forecast called for a reduction in educational training funds from NSF, without an obvious substitute, but at the same time the expanded research programming in which OTS served as the recipient institution for individual investigators promised sufficient funds from indirect costs to maintain the administrative structure. With hindsight we can say now that OTS was skating on thin ice. Virtually all of its funds were coming from a single source, namely NSF, and there was no endowment and little reserve. Furthermore, Spencer's attempt to institute station and vehicle rental fees at break-even levels was rebuffed by many investigators. For the sake of harmony and with the hope of fostering increased usage of the facilities, station rates were reduced to cover only the food costs. The expectation or hope was that the indirect costs from grants would cover the deficits.

The national crisis in Federal support for higher education peaked in the summer of 1971 with the resignation of the chief of the Education Directorate at NSF (Spencer 1971). Eight OTS courses were offered this year, but the projections for 1972 and 1973 looked foreboding. At the peak of course offerings in 1970, slightly in excess of $400,000 was provided by NSF for the education programs, whereas only $261,000 was granted for the 1972-1973 period. This ominous sign forced the Executive Committee to rule for a "stretch-out" of the funds and reduce course programs to four in 1972 and two in 1973. The problems of education funding were ameliorated to some extent by the success OTS was having on other fronts. A research laboratory building was added to La Selva, and construction of the Palo Verde field station was far enough along in the summer of 1971 to handle two courses. This same timeframe marks the building of the Comparative Ecosystem study (see section on Research). The infusion of major research funding through

OTS stimulated a tremendous amount of start-up activity, with the College of Forestry under J. S. Bethel's deanship at the University of Washington taking the lead to install baseline forest plots and environmental monitoring equipment. It was at this time also that Kenneth J. Turnbull was identified as the team captain for future research efforts on the Ecosystem Comparison project.

The research theme played an increasingly prominent role during 1971 with the completion of laboratory facilities at Palo Verde and La Selva for the Ecosystem Comparison study, and with the attraction of numerous graduate students and young faculty through the OTS Pilot Research Program funded by NSF and the Ford Foundation. There had been a long-felt need for better communication between the visiting scientists and local community, and by 1971 a critical mass of resident researchers prompted Benjamin H. Waite, the Assistant Director for Academic Affairs, and post-doctoral fellow Paul A. Opler to organize a monthly seminar series at UCR. The emerging prominence of the tropical programs led to an invitation from the International Biological Program (IBP). Howard T. Odum, chairman of the IBP Tropical Biome planning committee, proposed that IBP and OTS co-sponsor an integrated research program directed at tropical forests. The proposal was given serious consideration, but was finally rejected ostensibly because OTS's comparative ecosystem research program encompassed a broad range of interests that were directed to "validation" of models, rather than the creation of a new one "de novo" for the Tropical Biome (Spencer 1971). The high point of OTS's venture into ecosystem research was marked by a formal series of seminars presented to the Board of Directors at their annual meeting in November 1971 at Turrialba.

There were a lot of irons in the fire, but 1972 started out on a downbeat with Spencer's forecast of indirect cost income deficits for fiscal year 1972 and 1973 (Stone 1972a). Any shortfall in grant overhead that funded the OTS administration would deplete institutional funds and decrease program flexibility. Nevertheless, plans were moving ahead on phase III of the Ecosystem Comparison study, and a proposal was developed by Monte B. Lloyd's Research Committee for submission to the Ford Foundation on "A Coordinated Educational Program in Ecology for Latin American Students." There is a bit of déja vu here because they also proposed, as we are doing again in 1986, to organize a course for Costa Rican decision makers that would use the country as a model system in showing the interplay between human demography, agriculture, land use, economic development, politics, and law.

The final steps to acquire Las Cruces were negotiated at this time, and Campabadal and Waite investigated the feasibility of OTS's renting cloud forest property at Monteverde. An undercurrent of friction surfaced between Spencer and the "young Turks" scheduled to coordinate the courses (Emmel

1986), and the Executive Committee was asked to take a stand on the control of course budgets and composition of the faculty. The fact that the Executive Committee came down on the side of the course coordinator was negative enough in itself, but the rift with the Executive Director was widened when the Executive Committee voted in effect to close the NAO: "The maximum possible amount of OTS function presently carried out by the North American office be shifted to San José, Costa Rica, and that those operations which must be carried out in the United States be shifted to a member institution by the end of fiscal year 1972, if possible" (Stone 1972a). This action precipitated the letter of March 27 in which Spencer went public with his side of the story and was followed up, at the request of President Joseph M. Reynolds, with an audit of the NAO records by OTS Secretary-Treasurer Donald E. Stone and Duke University Treasurer Stephen C. Harward. The financial review of April 10 and 11 determined that the current "undivided surplus" of $29,000 would be reduced to $10,000 by June 30. Harward and Stone recommended the adoption of a new accounting system that would give better checks and balances and insight into the financial picture. This report was presented at the Executive Committee meeting of May 1 along with S. B. Preston's poll of the member institutions about their reaction to the proposal to disband the North American office (Stone 1972b). The sum total of the actions and remarks by the Executive Committee precipitated J. T. Spencer's resignation.

The Turnbull Era, 1972-1976

There was a cloud over OTS when Kenneth J. Turnbull was asked to step in. The organization was solvent, but expectations and demands outstripped financial resources (Stone 1973). The 1972 period was the penultimate year for course support from NSF. The usufruct agreement with R. G. Wilson gave OTS title to Las Cruces along with new responsibilities and headaches. The opportunity to acquire land at Monteverde had to be shelved as did plans for building new quarters on the UCR campus, and B. H. Waite's position of Assistant Director of Academic Affairs was terminated.

The NAO staff was trimmed from eight to two and one-half in the fall of 1972, and in January 1973 the accountant and part-time secretary were moved to smaller quarters in Miami. More responsibilities were heaped on Campabadal and the CRO while Executive Director Turnbull maintained residence in Seattle, Washington and commuted frequently to Miami. Retrenchment created demands for reorganization on all fronts and Turnbull found himself under great pressure from the OTS community to meet expectations that had been developed during the first decade of operation. S. B. Preston's tenure as president during this period was crucial because he knew OTS well from his early association as executive director, and he had gained

the contacts and respect of the OTS constituency. Still, Turnbull was on the hot seat. M. E. Mathias served as the buffer with R. G. Wilson at Las Cruces where expectations were high for the development of the botanical garden because of a three-year matching grant that was in hand from the Stanley Smith Horticultural Trust. La Selva had expanded too in the five years under OTS ownership. Facilities and trails had been improved and usage by researchers and courses had increased substantially. Since communication between the resident researchers and the OTS Board was viewed as a problem, Gary S. Hartshorn, predoctoral candidate at the University of Washington, was designated as Chairman of the Field Research Committee and invited to attend the Executive Committee meetings.

The pared-down graduate education program continued to sparkle as OTS's crown jewel (Pfeifer 1973). Orley R. Taylor helped the cause with a balanced budget as course coordinator of the No. 73-1 Fundamentals course and Mary F. Willson and C. E. Schnell successfully handled the summer program. Various suggestions were proposed to offer OTS-affiliated courses with member institutions taking the lead in the organization and financing. While this outlet might have picked up some of the slack in education, no sustained cooperative programming developed. The Comparative Ecosystem program was also under fire at NSF. The OTS umbrella proposal involving investigators with diverse research projects was judged inappropriate for the Ecosytem Program at NSF, and future proposals would have to be submitted to the General Ecology Program for review on a project-by-project basis.

The first Ecología de Poblacíones course, organized by F. Gary Stiles, Douglas C. Robinson, and Sergio Salas, was co-sponsored with UCR in the winter of 1974, and Tropical Parasitology and the Fundamentals course were offered in the summer. A decision, prompted by a persuasive presentation by researcher Gordon W. Frankie, was made by the Executive Committee to increase the buffer around La Selva, and in 1972 a narrow strip (Annex A) was added on the east side; and then again in 1974 some $22,500 was obligated to acquire 87 ha on the south boundary (Annex B). Construction of a two-story annex to the central station building was undertaken to move some of the long-term researchers out of the dormitory into semi-private quarters and to provide screened laboratory workspace. These activities were visible signs of progress in the programs and facilities in 1974. Even the financial picture seemed to end on a positive note when Treasurer William E. Wright reported that a recent NSF audit gave OTS a "clean bill of health" (Langenheim 1974). Efforts to further streamline the NAO administration resulted in the closing of the Miami office on December 13 and consolidating the records at Seattle with Turnbull and a full-time secretary and accountant.

The year 1975 started on a high note with a planning conference and symposium on The Ecology of Conservation and Development in Central

America and Panama (Chavarría 1976) organized by Charles F. Bennett on behalf of OTS and the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT), presided over by Rodrigo A. Zeledón. Warnings from NSF about financial accountability had surfaced earlier, but by midyear OTS was asked to present a formal statement of accounting procedures. Price Waterhouse & Co. was retained for this purpose in anticipation of an annual certified audit (Langenheim 1975). The second of three installments fell due on Annex B at La Selva and the annual $12,000 match of the Stanley Smith Horticultural Trust (SSHT) grant for Las Cruces was straining the system. Further pressures were created when NSF's William E. Sievers of the Research Resources program made a site visit to the three OTS field stations in November 1975, and concluded that only La Selva had sufficient ongoing research to be competitive for future funds. This pronouncement came as a shock to the Executive Committee and led the members to table a motion calling for continuation of the SSHT matching grant. The Board of Directors subsequently voted to reduce expenditures at Las Cruces to the contractual obligations with R. G. Wilson and related minor costs, and left open the option of canceling the SSHT grant if OTS matching funds could not be waived.

The year 1975 ended on a financial downbeat that was not fully appreciated by the Executive Committee until President Savage initiated a series of conference calls in January 1976 and followed these up with a letter to the Board on March 19 (Savage 1976a) and a meeting at the University of California at Los Angeles on March 30 and 31 (Douglas 1976). The bottom line was that OTS had accumulated debts in excess of $200,000 and a "cash flow" problem was triggered by NSF's unwillingness to release any more funds until the financial difficulties had been solved. As noted above, OTS had been "borrowing from Peter to pay Paul" for some years and the cycle was abruptly halted by NSF action. The fact that expenses exceeded revenue was no doubt exacerbated by OTS's inadequate accounting procedures and the consequent inability to monitor cash flow among the NAO (Seattle), the CRO (San José), and the subcontracts being administered for researchers at: USC, Los Angeles; UC, Berkeley; University of Texas, Austin; Texas A&M University, College Station; University of Michigan, Ann Arbor; and Florida State University, Tallahassee (see section on Research). Warnings to this effect had been raised by NSF as far back as 1974 and were detailed to the OTS administration in a meeting in Washington in May 1975 and a followup report (Ellis 1976). When the Executive Committee became aware of the gravity and protracted nature of the situation, Turnbull was asked for his resignation and a three-person management committee, consisting of President Savage, Vice-President C. F. Bennett and Treasurer J. Knox Jones, assumed interim administrative control and responsibility for developing a reorganization plan.

The Crisis of 1976

A quick fix for OTS's de facto bankruptcy was not in sight. NSF Grants Officer Gaylord L. Ellis had invited OTS representatives to a meeting on March 15 at which NSF concluded that "it would be necessary for OTS to come up with a formal management plan which would provide assurance of their ability to deal with creditors without the possibility of being forced into bankruptcy and also indicate implementation of procedures demonstrating that the organization is being operated on a sound fiscal and administrative basis" (Kruithoff 1976). The discouraging outcome of this meeting was reported to the Executive Committee in a conference call on March 17, and the stark reality of survival was seriously questioned. Savage and Bennett estimated that a minimum of 20 institutions would have to be willing to accept an annual dues increase from $2,000 to $5,000 and the creditors would have to grant OTS time to repay the debts. Failing this, the alternative plan for bankruptcy would have to be activated (Savage 1976b). The prospects seemed slim, but the first thing that had to be done was to re-establish credibility with NSF. At this point I approached Duke Chancellor John O. Blackburn, Treasurer S. C. Harward and Graduate Dean John C. McKinney with the request to provide financial expertise in order to evaluate the crises and to consider having Duke serve as fiscal agent of OTS, if this seemed desirable. Approval of Duke involvement came with the letter of March 19, in which President Terry Sanford told NSF Director Guyford Stever that the University "would be willing to assume leadership in developing a plan to put OTS back on sound financial footing" (Sanford 1976).

The pressure for urgent action continued to mount with the ongoing operation in Costa Rica. Contractual obligations for La Selva land purchases totaling nearly $14,000 were coming due; the annual Las Cruces obligation of $3,600 could not be overlooked; and $20,000 in unpaid bills had accumulated (Campabadal 1976a). Some of the creditors were forestalled by selling off several vehicles in Costa Rica, but even a subsistence level of operation was estimated to cost $5,000 monthly (Campabadal 1976b). The UCLA meeting of March 30-31 tallied the OTS liabilities at $215,890 and reviewed a reorganization plan that proposed to establish the president as the chief executive officer and shift the day-to-day operations of OTS to the resident director in Costa Rica. Fiscal management would be controlled by contractural arrangements with a member institution whereby 50% of an administrative manager's salary would be covered. UCLA, USC, and Duke were mentioned as possible fiscal agents. UCLA was ruled out because of the perceived bureaucratic inflexibility of state institutions, leaving USC and Duke to approach NSF about the ground rules for reorganization. The Duke administration took responsibility for setting up a meeting with NSF officials for

April 14. President Savage was accompanied by Clark McCartney, a Grants and Contracts officer from USC, and Duke sent Treasurer S. C. Harward and myself. The NSF administrators indicated that a six-month interim La Selva maintenance grant would be considered if Duke University assumed responsibility as fiscal agent of OTS and if the following conditions were met by the referenced target dates: (1) by April 24, 1976 the President of OTS shall provide NSF with written evidence that the OTS creditors will delay for one year the [request for] payment of OTS debts; (2) by May 1, 1976 Duke University shall submit to NSF a proposal for the operational support of the OTS Costa Rican field station facilities, including a brief statement of Duke's contributions toward the management of the research activities; and (3) by May 14, 1976 OTS shall submit evidence of the willingness of OTS member institutions to increase annual membership dues to $5,000 per institution (Savage 1976c). Shortly after the meeting I was appointed interim Executive Director and given the challenge of putting OTS back on its feet. With good fortune the conditions were met on schedule, albeit with the loss of Illinois and Texas A&M, and W. E. Siever's Research Resources program at NSF recommended a six-month grant of $80,000. These funds permitted OTS to stabilize its administration and the La Selva field facility. The road back to financial health was relatively rapid, but painful, because the repayment of debts had to be squeezed from institutional dues and other non-governmental sources of income. This last financial crisis had its good points in re-acquainting member institutions with OTS, but there were some scars left as well. Turnbull in particular resented the fact that his efforts on behalf of OTS were not appreciated (Turnbull 1976). He was particularly bitter about the official NSF records, disclosed through the Freedom of Information Act by Science Trends, that failed to acknowledge the Foundation's lapses in proper financial management which he felt had contributed to the crisis (Anon. 1976).

The Stone Administration, 1976–

The survival of OTS during the crisis of 1976 and its growth and development over these past ten years are events of great importance, but they are obviously far too close for me to assess objectively. Nevertheless, I will relate my historical tie to OTS and some of the documented facts that provide background for a future exposé.

I first became involved with OTS as a student in the 1965 course in Advanced Botany on tropical monocots. This was during the period when the course participants consisted of graduate students and young faculty who were hoping to gain experience in tropical biology. I was on the staff at Duke University at the time and had already developed field research plans that included Costa Rica. My course exposure was enough to convince me that

the University should become a member of the consortium, and when it joined in 1968 I was appointed to serve as one of the institutional representatives. Active interest in the affairs of the organization led to my election to the Executive Committee in 1969 and continued through 1976. In December of 1975 I volunteered to write an OTS proposal for a newly created NSF program in Research Initiation and Support (RIAS). This experience deepened my understanding of the OTS operation at a very fortuitous time, and ultimately proved to be the funding salvation for the 1976 Fundamentals course. Henry A. Hespenheide of UCLA had agreed before the crisis to serve as coordinator, but OTS obviously was in no position to make any guarantees. Fortunately, Hespenheide was willing to wait until a firm commitment could be made. The favorable eleventh-hour decision by the NSF Science Education Directorate to fund our RIAS proposal ($240,000/four years) breathed new life into the educational programming and complemented the interim La Selva grant to carry OTS through its bleakest hour.

Reconstructing the financial debacle was a first step in restructuring the OTS administration. S. C. Harward and I reviewed the NAO records in Seattle in late April 1976, and in June the files were trucked to quarters at Duke University in Durham, North Carolina. Picking up the loose ends and figuring out the bases for our financial obligations was like working a Chinese puzzle. Harward personally undertook the task of establishing a double-entry bookkeeping system for OTS and reconstructing the financial past, while Beverly L. Stone assumed responsibility for deciphering the files and running the NAO. Since many of the day-to-day operational tasks had been transferred to Costa Rica, a review of finances sent Robert W. Hughes (Duke Sponsored Programs), Stanley D. Gunsher (NSF Cost Analysis), W. E. Sievers (NSF Research Resources) and myself to CRO in early May. As a result of this audit and a subsequent site-visit by Harward, the administration of OTS finances was centralized at NAO, and CRO expenditures were limited to an imprest fund that was replenished out of NAO on the basis of paid invoices. Duke predoctoral candidate Lucinda A. McDade was installed as station manager at La Selva to provide administrative control and direct feedback to NAO. The implementation of tighter financial control and stronger administrative directives gradually took their toll on the CRO, and in January 1978 Jorge R. Campabadal resigned as Resident Director. The international scientific community was both shocked and saddened by Campabadal's departure because he had seen OTS through 11 years of phenomenal growth. He was personally responsible for the on-site development of facilities at La Selva and Palo Verde, and he served as the master logistician to courses and researchers. Campabadal was a friendly bilingual voice of wisdom to nearly a thousand OTS course participants.

The year 1978 got off to a rocky start with Campabadal's resignation but ended on a good note. Secretary Flor M. Torres was elevated to Chief of Operations, and by November OTS had retired its past debts and established financial accountability with an annual certified public audit. The benign neglect of Las Cruces stimulated R. G. Wilson to look elsewhere for maintenance of the botanic garden, and various proposals were put forth to transfer title and management of the property to some responsible local organization. Harvard predoctoral candidate Thomas S. Ray, Jr. became the La Selva station manager and vigorously campaigned with Costa Rican government officials for extending Braulio Carrillo National Park by a corridor to connect with La Selva (Bentley 1978).

From 1979 onward, OTS has continued to build on its strengths of graduate education and research. Much of the credit for OTS successes in Costa Rica during this growth phase goes to Chief of Operations Torres, and by 1980 Station Co-Directors David B. Clark and Deborah A. Clark shared the excitement of new developments at La Selva. When Torres resigned in 1983 to join her husband in Switzerland, Charles E. Schnell was coaxed away from his professorship at the Universidad Nacional to head up the CRO, and more recently to assume responsibility as Resident Director of all OTS operations in Costa Rica.

At the time of this writing, OTS has overcome its administrative shortcomings and moved forward to establish a distinguished record. True to its mission, OTS has provided leadership in education, research, and the wise use of natural resources in the tropics. The next two sections highlight OTS's success that traverses the tenures of ten presidents (Table 2) and seven chief executive officers (Table 3).

EDUCATION

The success story of OTS to date is based largely on its contribution to graduate education in tropical biology. True to its original purpose of training a cadre of scientists who were knowledgeable about tropical studies (Gomez and Savage 1983), OTS has taught over 1,600 participants since the first course in the summer of 1964. Nearly 100 courses have been offered in more than a dozen fields (Appendix 1), but Tropical Biology: An Ecological Approach, more familiarly known as the Fundamentals course, has been the mainstay that has entertained the greatest audience and has received the widest acclaim. It is in fact the bread-and-butter program that most institutions use to justify membership in the consortium. Interestingly, OTS retains neither resident faculty nor research scientists to maintain the programs. Instead, we have been able to rely on the unparalleled pool of scientific talent from the faculties within and outside the consortium, and to utilize their

talents through release-time arrangements with the home institutions for the short-term visiting faculty or by limited hiring engagements with the full-time coordinators not otherwise salaried.

The Fundamentals course has a truly unique design that evolved from a typical lecture, laboratory, and occasional field-trip experience into a program whereby the field served as the classroom, and lectures on ecological theory and organisms revolved around hands-on experience with a series of tropical ecosystems. The evolution of this intensive, interactive format was favored by the opportunities afforded in Costa Rica to witness firsthand a diversity of tropical habitats, as well as the disgruntlement expressed by the first course participants (Janzen 1986), but the intellectual nudge to actually do so has to be credited in part to visiting faculty such as C. D. Michener (1964) and graduate teaching fellow Stephen P. Hubbell (1965) who articulated the need for taking advantage of the wonderful field opportunities. With this encouragement and the natural history bent and enthusiasm of D. H. Janzen and Norman J. Scott as the principal contributors to the course between 1965 and 1970 (Appendix 1), a workable format was developed that raised the courses to a new level of excitement and excellence.

The course design has in fact remained largely unchanged to the present time. After a few days of orientation lectures in San José, the 20 or so budding scientists, who have been selected by competition from among the world's leading graduate institutions, head to the field for nearly eight weeks of "total immersion." While this schedule sounds like an arena for testing survival of the fittest, proper orchestration by the course coordinators and rotation of visiting scientists with expertise on the sites results in a highly intense, intellectually and physically exhausting training program that invariably produces student reviews stating that "this is the best graduate course ever experienced." No doubt part of the attitude is generated by the esprit de corps that emerges from the group interaction under such trying conditions. Also one has to credit course design. From two to twelve days are spent in four to five contrasting tropical ecosystems selected from a rich assortment of pristine and disturbed sites throughout Costa Rica (Fig. 1 and Janzen 1983). Dawn-to-dusk work ethics combine theory in lectures with research-oriented field problems for both individuals and groups. Writeups, analyses, presentations, and discussions are all part of the intense dialogue. There is no escape for students or instructors alike: habitats, organisms and ideas are everywhere and in an overwhelming abundance and diversity .

The value of an OTS course goes far beyond the immediate gains of a tropical experience, eight graduate credits, and a foot in the door on tropical research. The collegiality developed here often leads to tight personal bonds that have significant professional implications down the line. The highly select student body and faculty of each course come from a wide range of

Fig. 1. Organization for Tropical Studies training and research sites.

top-flight institutions, and the opportunity for exchanging ideas and scientific techniques is unparalleled. Furthermore, this interchange between "tomorrow's leaders" constitutes a vast scientific network that has already had a substantial impact on Costa Rica and the United States in raising the level of scientific understanding about tropical biology. OTS alumni and faculty occupy distinguished positions throughout the academic community, and are in key decision-making jobs in governmental agencies as well as many of the advisory and consulting groups that affect government policy. We have every reason to believe that the influence of OTS training programs will continue to grow as new efforts are launched to link the academic knowledge of tropipical systems with the decision maker's domain of natural resources.

RESEARCH

Where education stops and research starts is a moot point. The OTS courses have a strong problem-solving component, and the participants are primed to conduct research as part of their graduate programming. The initial, and in some ways most important, link OTS has forged with research is through the "pilot study" awards to young postdoctoral investigators and graduate students. Between 1967 and 1970 the Ford Foundation and NSF provided $250,000 to support 91 projects whose diversity exceeded even that of the courses (Appendix 1). When the NSF award ran out in 1969 and the Ford grant in 1970, OTS was without pilot research funding until 1976 when the NSF program in Research Initiation and Support (RIAS) breathed new life into post-course research projects. RIAS support ($240,000) terminated in 1980, but the slack was picked up by the Jessie Smith Noyes Foundation that has provided block funding ($442,500 to date) to OTS for competitive research fellowships for graduate students and a small number of postdoctoral scientists. Hundreds of young researchers have thus been afforded the opportunity to bridge the gap between the courses and nascent research programs in the tropics.

Efforts by OTS to establish a formal research program date back to June 1968 when a two-year $450,000 NSF grant was awarded to conduct "An ecological study of a wet and dry forest ecosystem in Costa Rica." The primary stimulus for this venture came from Dean J. S. Bethel and his colleagues in the College of Forestry at the University of Washington and J. M. Savage, University of Southern California (Baker 1986). With La Selva as the wet forest research center and Palo Verde as the dry forest site (Fig. 1), the overall scientific goals were to inventory the biological and environmental parameters and then conduct a host of multidisciplinary studies that were centered on three research themes—primary productivity, plant reproductive biology, and insect dynamics (Spencer 1970:48-63).

The establishment and inventory of La Selva and Palo Verde was tremendously difficult because of the inaccessibility of the sites and the harsh climatic conditions. This aspect of the program was generally successful in that it laid the foundation for La Selva's preeminence as a biological field station. Boundaries were established and surveys were completed of the geology and soils at La Selva and Palo Verde. Coarse topographic surveys were done for La Selva and a 200-meter grid system was installed by H. Riekerk. Also, three intensive study areas of four hectares each were marked off into 20m x 20m plots wherein all trees were identified and the diameters measured by W. H. Hatheway and G. S. Hartshorn. During late 1970 a weather tower was erected at La Selva and dendrometers were installed on about 50 select trees. An automatic monitoring system was designed by L. J. Fritschen to capture and integrate weather and tree growth data by using battery-operated data-loggers that stored the information on magnetic tape. This pioneering effort to employ sophisticated instrumentation in the tropics was fraught with technical problems and the results were expensive and limited.

The research component of the Comparative Ecosystem study extended over three NSF umbrella grants between 1968 and 1976 and a series of individual awards involving a changing cast of scientific participants. In the first phase J. S. Bethel coordinated the studies on primary productivity with foresters from the University of Washington: biometeorology, L. J. Fritschen; soils, mineral cycling and plant nutrition, D. W. Cole, S. P. Gessel, J. G. McColl; cell and tree growth, J. S. Bethel, K. J. Turnbull; and plant community interaction, W. H. Hatheway. The studies on plant reproductive biology were shared by H. G. Baker (University of California, Berkeley) and G. W. Frankie (Texas A&M University). The program in the dynamics of insect populations was developed by D. H. Janzen of the University of Chicago and assisted initially by A. M. Young.

Research accomplishments during the first two years of the ecosystem grant were varied and coordination between the research teams met with limited success. At the time of the renewal request, funding through the umbrella proposal was narrowed to the primary productivity group and the plant reproductive biology team. Janzen and several other investigators continued to lend their names in support of the ecosystem umbrella while submitting separate proposals through OTS. In 1970, for example, Janzen was funded by NSF for a study on "Plant-insect interactions," Emmet T. Hooper (University of Michigan) and Theodore H. Fleming (University of Missouri, St. Louis) for "Small mammal faunas of two tropical rain forests," and Monte B. Lloyd (University of Chicago) for "Tropical forest litter community." This independent mechanism for handling grants was continued until 1976 for Janzen's research on the "Effects of herbivory and seed predation on tropical plants" and Donald R. Strong's (Florida State University)

work on "Hispid beetles and their Zingiberales hosts in Tropical America."

The second phase of the Ecosystem Comparison study was begun in 1970. The principal scientists from the first round remained affiliated, but there were some adjustments in personnel. K. J. Turnbull replaced Bethel as the team leader of the primary productivity studies and postdoctoral fellow Paul A. Opler became affiliated with Baker and Frankie on their plant reproductive biology project. This was also the period that Kamaljit S. Bawa, postdoctoral fellow at the University of Washington, received OTS Pilot Research support to work on the "Chromosome number and meiotic behavior" of rainforest and dry forest tree species. Considerable momentum and international interest was generated by OTS's fledgling attempt to engage in ecosystem-level research, but the task of keeping the projects on track proved to be difficult. The umbrella concept was fine in principle in that it gave core administrative and facilities support to field centers used by many. It proved less satisfactory, however, in developing the best possible scientific proposals for inclusion in the umbrella package, and it failed miserably in pulling the subprojects together in any semblance of an integrated ecosystem analysis (Cooper 1970).

Stimulated in part no doubt by the demise of funding for graduate education in the early 1970s, the research arm of NSF provided strong encouragement for OTS to develop sound, productive programs in tropical biology. At the same time it was clear that the research umbrella was unraveling at the fringes. The final phase of the Ecosystem Comparison support was granted in 1973 for a three-year period. Even at this time, however, new research teams were attracted to the fold: Lawrence E. Gilbert (University of Texas, Austin) focused on passion flower vines as the single primary producer for *Heliconius* butterflies; Gordon H. Orians (University of Washington) and G. S. Hartshorn (University of Washington) examined the role of tree-fall gaps in tropical forest dynamics; J. M. Savage (University of Southern Caliornia) and Ian R. Straughan (University of Southern California) investigated the community structure of the leaf-litter herpetofauna; and Henry S. Fitch (University of Kansas) launched into a study on the reproductive cycles, population, structure, biomass and food in vertebrate consumers. Even with these sound additions, the crux of the umbrella-proposal problems did not go away. The nagging uncertainty as to the best way to structure a coordinated research effort was still there, but even more damning was the paucity of published research papers by the primary productivity group. At the same time, the plant reproductive biology researchers flourished, particularly in the dry tropical ecosystem, and a long series of symposia contributions and papers have enriched our knowledge about tropical plant biology.

OTS's venture into managing ecosystem level research ceased during the financial crisis of 1976 and was not revived until 1984 (see next section). OTS's encouragement and facilitation of independent research in Costa Rica

and at OTS field stations in particular has been relatively unaffected over the years by the many trials and tribulations detailed above. Hundreds if not thousands of researchers have been assisted by OTS, and the scientific literature, some of which can be found cited in *Costa Rican Natural History* (Janzen 1983), is rich in acknowledgements to the many OTS staff who helped make the research possible.

OTS TODAY

OTS draws from the strength of its present membership of 40 institutions: 34 of which are U.S. universities, and the balance includes the Smithsonian Institution, the University of Puerto Rico, and four institutions from Costa Rica (Table 4). Each institution currently pays $5,500 in annual dues (FY 87) and appoints two members to the Board of Directors. The board elects a 12-person Executive Committee (Table 5) and this group in turn hires and fires the Executive Director. The North American headquarters (NAO) has been located at Duke University in Durham, North Carolina since the last financial crisis in 1976. From here a seven-person staff initiates the planning, coordinates the programming, keeps the audited fiscal records, and handles the fund-raising for our various activities. Costa Rica is the logistic and operational base, and it was selected as such in the early 1960s because the country is small, about the size of West Virginia, exceedingly rich in habitats and biota, politically stable as a democratic republic and most supportive of the goals that OTS espouses (Hubbell 1967).

Costa Rica proved to be a wise choice on all counts, and particularly in regards to local support. The strength of our Costa Rican relations has grown over the years into a healthy, working relationship that operates at many levels. Our library, for example, invites use by local students writing reports on tropical biology, and the OTS courses in both English and Spanish have touched the lives of virtually all field biologists in Costa Rica. We are privileged to have the three graduate degree-granting institutions (ITCR, UCR, UNA) and the Museo Nacional as OTS members, and we enjoy their collegiality in education and research. José Andrés Masís, Director of the Planning Office of the Council of University Rectors (CONARE), currently serves on the Executive Committee of OTS as Vice President for Costa Rican Affairs and Chairman of the Costa Rican Institutions Committee (CRIC). Previously, this important position had been held by Rodrigo Gaméz, Director, Cellular and Molecular Biology Research Center, UCR; Rodrigo A. Zeledón, former course coordinator of 1964-2, longtime President of CONICIT and current Minister of Science and Technology; and Manuel M. Murillo, alumnus of the 1964-1 course and Director of the Center for Marine Sciences at UCR. These outstanding individuals have brought great insight and wisdom to the OTS

TABLE 4. OTS MEMBER INSTITUTIONS 1986-1987

University of Arizona
Auburn University
University of California (System)
University of California, Los Angeles
University of Chicago
City University of New York
University of Connecticut
Cornell University
University of Costa Rica
Duke University
University of Florida
University of Georgia
Harvard University
University of Hawaii
Indiana University
University of Iowa
University of Kansas
Louisiana State University
University of Maryland
University of Miami
University of Michigan
Michigan State University
University of Minnesota
National Museum of Costa Rica
Universidad Nacional Autónoma
University of North Carolina (System)
Pennsylvania State University
University of Puerto Rico
Rutgers University
Smithsonian Institution
Stanford University
State University of New York, Stony Brook
Instituto Tecnológico de Costa Rica
Texas A&M University
Tulane University
University of Utah
University of Washington
Washington University
University of Wisconsin, Madison
Yale University

in Costa Rica, and they are representative of the many friendships and working relationships OTS has established over the years.

The Costa Rican office (CRO) located in San José houses the Resident Director and a staff of twenty or so who worry about the logistics and operations of three field stations, the numerous training courses and scientific tour groups (Smith 1978), the hundreds of individual researchers and tourists who visit each year, and the far-reaching scientific and political issues that impinge on OTS's programs and well-being in Costa Rica. At times the San José office behaves like a spastic nerve center when simultaneous demands are placed on its limited resources. The 32-passenger bus and four-wheel drive vehicle fleet often have to be supplemented by outside rentals to carry the load, and the course field equipment and library reference books can only be divided so many ways before the office personnel and course instructors become frazzled. Mind you, all of this local logistic work is done under the constraints of another culture and at another pace. The fact that the office is outfitted with a copy machine and microcomputers with telecommunication capabilities does not speed up the purchase of nails or payment of bills.

The training and research activities of OTS are conducted at various sites throughout Costa Rica (Fig. 1), on both public and private land such as the

TABLE 5. OTS EXECUTIVE COMMITTEE 1986-1987

President	Peter H. Raven, Missouri Botanical Garden
VP Education	Barbara L. Bentley, SUNY, Stony Brook
VP Finance	Harold J. Michaelson, Smithsonian Institution
VP Development	Jay M. Savage, University of Miami
VP C.R. Coordination	José Andrés Masís, Council of Costa Rican University Rectors
Secretary	Richard K. Koehn, SUNY, Stony Brook
Treasurer	Richard A. White, Duke University
Members-at-Large	John J. Ewel, University of Florida Rodrigo Gámez, University of Costa Rica Gordon H. Orians, University of Washington G. Bruce Williamson, Louisiana St. University
Recent Past President	Thomas M. Yuill, University of Wisconsin, Madison

cloud forest reserve at Monteverde, the agricultural research center at Turrialba (CATIE), and many of the magnificent parks, but OTS's principal responsibility is to the management of field stations at Las Cruces, Palo Verde and La Selva. OTS got into the field station business before the park system was in place and at a time when only limited accommodations were available near the preferred study sites. Horror stories can still be heard about early course groups with Montezuma's revenge sharing a single stopped-up toilet in the town's best and only hotel. In 1968 OTS took steps to acquire La Selva, situated in the Atlantic lowlands of the Sarapiquí district; in 1969 a lease arrangement was worked out for a Pacific lowland dry forest site in Guanacaste Province, and the Palo Verde station was built at the base of limestone hills; and finally in 1983 an agreement was made to acquire Las Cruces Botanical Garden and Field Station in the coastal mountains of southern Costa Rica (Anon. 1972). Each of these field sites has contributed uniquely to the OTS programs, but for reasons discussed below, only La Selva Biological Station has come close to developing its potential as a world-class site for training and research (see also Clark 1988).

Why La Selva and not Palo Verde or Las Cruces? There are several contributing factors such as accessibility and inherent station management difficulties, but the bottom line is that research use of La Selva was sufficiently high

to maintain NSF's interest in providing continued funding for a tropical research site. La Selva is a truly biologically rich rainforest site, and one that should need no great deal of promotion. The fact of the matter is, however, that La Selva and OTS have been good for each other. In the early 1970s when NSF training funds for U.S. graduate students were phased out, OTS was able to lean more heavily on the development of La Selva as a center for tropical research. This move of course had positive repercussions in providing a site for graduate education, as well as carrying part of the burden for the OTS administration. At the same time La Selva benefitted from the intense but gentle research exploitation. The La Selva station and its environs became known as a tropical training center and as a site with great potential for research. The research usage has increased dramatically and in phase with the improvement of facilities: electric linepower was made available in 1978; a microwave telephone was added in 1979; a cable suspension foot bridge in 1982; large, central air-conditioned laboratories in 1983; and the list does not stop here. As research facilities improved more visitors were attracted, and this pressure in turn led to the need for better accommodations, a situation that has been addressed in 1986 by the completion of two new dormitories and a 72-person dining facility.

Facilities in themselves do not make great institutions, and the real credit to OTS has to be in its accomplishments in graduate training, research, conservation, and public service. While courses have ranged from forestry (Helms 1971) to pteridology (Mickel 1967), Tropical Biology: An Ecological Approach has continued to appeal to the broadest constituency. I should note here that a two-month OTS course for twenty students is not cheap; current direct costs are in the $50,000-65,000 range and this doesn't even include transportation for getting the students to Costa Rica! Fortunately the Andrew W. Mellon Foundation has been our course benefactor since the NSF/RIAS support phased out in 1980. In 1986 OTS offered four courses: two in Tropical Biology, Jan-Mar. and June-Aug., Tropical AgroEcology, and Ecología de Poblaciones. Future programming will continue to seek ways to incorporate fundamental biological information into courses that have relevance to our host countries in the tropics.

For some years, OTS had no provision beyond courses to aid young researchers getting started in the tropics (see Research); they were on their own once the course was over. Starting in 1980 OTS received generous funding from the Jessie Smith Noyes Foundation to support three levels of tropical research fellowships: post-course mini-research projects with awards up to $750; predoctoral pilot research projects in the $500 to $2,000 range; and both pre- and postdoctoral research projects that occasionally range over $10,000. Although OTS restricts these competitive fellowships to field research within Costa Rica, the important point is that young researchers

have a way into the national competitive scene where research proposal success is tied closely to prior experience and preliminary data sets. Research generated by OTS alumni and their academic progeny far transcends our current sphere of influence. Both the OTS programs in Costa Rica and those of the Smithsonian Tropical Research Institute in Panama have had tremendous impact on tropical research productivity, as measured by a survey of the literature and presentations at national meetings (Clark 1985).

To a large extent OTS's role in tropical research has been to provide the training, opportunity, and facilities. About eight years ago it became evident that a center such as La Selva could not be passive like a hotel and wholly dependent on the researchers who happened to drop by. To develop the full research potential of the site and provide some control over the usage and research direction, four research areas were identified that are particularly suited to La Selva and the potential clientele (LSAC 1978): systematic biology; evolutionary biology; physiological plant ecology; and ecosystem level studies. With this research framework in place, we were then able to assess to what extent the past research activities had utilized La Selva and, more importantly, what would be required in order to exploit fully the research potential of the site. About the same time, during the late 1970s, a National Research Council committee chaired by Peter H. Raven was preparing a document on Research Priorities in Tropical Biology (NRC 1980). Among other things, the distinguished panel of biologists recommended that ecosystem level research be concentrated at four sites in the world—one in Asia, one in South America, one in Mexico, and the La Selva Biological Station in Costa Rica. Of these, La Selva was the only site where NSF has had a long record of financial support.

The pump was primed by the publication of *Research Priorities* in 1980 to move forward in a major way in the development of new research programming at La Selva. Electricity and telecommunications were in, but most important was the establishment of full-time professional management when David B. and Deborah A. Clark were hired in 1980 as Station Co-Directors. They have been on site these past seven years to oversee the dramatic development of research facilities at La Selva and to stimulate research through intellectual leadership. Beyond the literally thousands of individual research projects on all aspects of plant and animal ecology, La Selva now supports experimental and ecosystem level research in several key areas, such as the role of Bushmasters as top predators; the physiological ecology of gap and understory tree species; the dynamics of tree-fall gaps (Gaps project); the nutrient availability in tropical soils as affected by man and nature (Plots project); and the demography and seedling dynamics of canopy trees (Trees project) (see Clark et al. 1987).

The first three programs of OTS that I have outlined—namely courses, fellowships, and research—constitute the core of our operation and the fabric that holds the consortium together, but I would be remiss not to recognize newly found directions that have evolved as a result of our efforts to interface with the real world. I am thinking here of two areas: conservation efforts related to Braulio Carrillo National Park, and public service projects that range from environmental education to contracts with the U.S. National Aeronautic and Space Administration (NASA). Our conservation efforts to date have been focused on La Selva and its environs for obvious reasons. One of the world's most prized tropical training and research sites was ever-so-surely being isolated by the colonization and resultant clearing of the Atlantic slope of Costa Rica by settlers looking for homesteads and by the large-scale loggers interested in profit. There was the virtual certainty of reducing La Selva to a small patch of forest surrounded by a sea of pasture. The whittling away of lush tropical rainforest reached a head in 1980 when a neighbor on the west flank threatened to log to the boundary of the 730-ha acre reserve. This challenge precipitated OTS's campaign to buy the adjacent 631 ha in 1981, and heightened our realization that immediate steps had to be taken to protect the vast Sarapiquí wilderness. While OTS is not a conservation organization per se, our interest in tropical training and research cannot overlook the need for suitable sites and the role they play in addressing natural resource issues.

Beyond the vested interest that OTS has in all tropical sites with potential for pursuing our broad-ranging programs, we have come to realize that obligations and opportunities exist to use our expertise in serving the welfare of mankind. Science for sustainable development is the catch-all for some of our newer projects. Included here is our work with NASA where they are trying to correlate data taken by satellites and airplanes with ground-truthing information provided by OTS on species composition and biomass along predetermined flight paths. Another example is the agreement with the Forestry Support Program of the U.S. Department of Agriculture to write a manual on agroforestry in Spanish that can be used to train Latin American technicians (OTS/CATIE 1986). Over the years OTS has sponsored or co-sponsored several scientific symposia, the most recent being in March 1985 on The Population Biology and Physiological Ecology of Mesoamerican Forests (Clark et al. 1987). OTS was intimately involved with the publication of the award-winning book *Costa Rican Natural History*, edited by D. H. Janzen (1983), and we have assumed responsibility for the Spanish translation. Perhaps the most important public service of OTS has yet to be realized. This responsibility has to do with efforts launched in 1984 in the field of environmental education. Our experience at La Selva in acquiring the neighbor's property in 1981, and the subsequent hassle with trespassers who

claimed historical right of passage, made us sensitive to the fact that land ownership is only as secure as local acceptance. To carry this idea a step further, a reserve or national park has a very limited half-life unless the local community has a vested interest in wanting and caring for it. For this reason OTS has initiated a variety of programs to reach the school children, teachers and parents in the Sarapiquí community adjacent to La Selva Biological Station and the Zona Protectora 'La Selva.' There can be no better investment for the long-term acceptance of Braulio Carrillo National Park.

The future may be limited by resources, but not by ideas and aspirations. Great opportunities are seen for course programs in agroecology and natural resources that involve greater participation of Latin American students. Exciting prospects also exist for tailoring some of the tropical programs for governmental decision makers who lack the basic ecological knowledge pertinent to passing judgement on key environmental issues. As the research at La Selva expands to encompass a greater diversity of approaches, we can expect this site to be in the vanguard of those seeking integration of the knowledge of population processes into a theory of how ecosystems work (Ehrlich 1986).

One might rightfully ask if the administrative foibles documented in the historical profile have prevented OTS from achieving its professed goals of providing leadership in education and research, and the wise use of natural resources in the tropics. I judge not, based on the following criteria. Foremost, no doubt, are the 1600 alumni and hundreds of OTS faculty who constitute the core of the New World expertise in tropical biology. The influence of the OTS programming is felt throughout the private and public sector. OTSers are omnipresent from consulting firms, to universities, to government offices. OTS-sponsored research, research facilitated by OTS, and research stimulated by OTS courses and programming is leaving a legacy of scientific reports as building blocks for human inquiry into the nature and functioning of tropical ecosystems. The very presence and activity of OTS has captured the scientific and public attention and has made us all very aware of the wonders and the fragility of the ecosystem we call Earth. In recognition of the role of OTS in "advancing the understanding and protection of threatened tropical ecosystems," the Tyler Prize Committee named OTS as co-recipient of the 1985 John and Alice Tyler Ecology-Energy Prize, and presented OTS President Peter H. Raven with a gold medallion and a $75,000 check. I should note that $50,000 of this prize was turned over to the Nature Conservancy for preserving the Zona Protectora. One would have to conclude that OTS has been successful in spite of itself because of the purity of its cause and the dedicated commitment of some truly outstanding individuals.

ACKNOWLEDGMENTS

First, it is appropriate to note that I have had privileged access to the historical files associated with the North American Office of OTS. Beyond this primary source, useful critiques and comments have been provided by Beverly L. Stone and Lucinda A. McDade of NAO, Charles E. Schnell of CRO, and long-time associates of OTS who have served variously as students, course coordinators, faculty, Board of Directors and administrators: Herbert G. Baker, Thomas C. Emmel, Gordon W. Frankie, Daniel H. Janzen, Mildred E. Mathias, Stephen B. Preston, Reed C. Rollins, Jay M. Savage, and Jack T. Spencer. I am particularly appreciative of their comments and personal insights that helped me identify historical highlights. Choice of the facts to be emphasized and judgment about their meaning are, of course, mine.

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*All unpublished memos, letters, and reports are bound in volumes referenced to this paper and deposited in Archives, Perkins Library at Duke University and are on reserve at the NAO.

APPENDIX 1. OTS COURSES, 1964-1987

Year	Number and Title	Coordinator
1964	1 Tropical Biology: An Ecological Approach	J. L. Vial, Univ. Costa Rica
	2 Research Participation	R. A. Zeledón, Univ. Costa Rica
	3 Biology & Evolution of Tropical Plants	R. Ferreyra, Univ. San Marcos de Peru
1965	1 Tropical Biology: An Ecological Approach	L. R. Holdridge, Tropical Sci. Ctr.
	2 Tropical Forest Ecology	P. W. Richards, Univ. North Wales
	3 Tropical Biology: An Ecological Approach	D. H. Janzen, Univ. of Kansas
	4 Advanced Botany (Monocotyledons)	P. B. Tomlinson, Fairchild Tropical Garden J. Idrobo, Univ. Nac. Colombia
	5 Biology of Tropical Insects	C. W. Rettenmeyer, Kansas St. Univ.
1966	1 Biology of Tropical Vertebrates	E. T. Hooper, Univ. Michigan
	2 Biology of Tropical Epiphytes	C. H. Dodson, Univ. Miami
	3 Tropical Biology: An Ecological Approach	N. J. Scott, Univ. Costa Rica
	4 Biology of Tropical Grasses	C. Calderón, Smithsonian Instit. R. W. Pohl, Iowa State Univ.
	5 Tropical Biology: An Ecological Approach	L. L. Wolf, Syracuse Univ.
	6 Tropical Biology: An Ecological Approach	G. S. Daniels, UCLA
1967	1 Advanced Zoology (Insect Ecology)	D. H. Janzen, Univ. Kansas
	2 Tropical Biology: An Ecological Approach	R. J. A. Goodland, McGill Univ.
	3 Geography	R. N. Pearson, Univ. Michigan
	4 Advanced Botany (Pteridophytes)	J. T. Mickel, Iowa State Univ.
	5 Tropical Biology: An Ecological Approach	T. C. Emmel, Stanford Univ.
	6 Tropical Biology: An Ecological Approach	M. E. Mathias, UCLA R. L. Rudd, Univ. Calif. Davis
1968	1 Tropical Biology: An Ecological Approach	N. J. Scott, Univ. So. Calif. T. C. Emmel, Univ. Texas
	2 Problems in Tropical Forestry	T. Waggener, Univ. Washington
	3 Crop Plants in a Tropical Environment	C. O. Hesse, Univ. Calif. Davis V. W. Carlisle, Univ. Florida
	4 Reproductive Biology in Tropical Plant Ecology	H. G. Baker, Univ. Calif., Berkeley
	5 Tropical Biology: An Ecological Approach	N. J. Scott, Univ. Connecticut
	6 Tropical Biology: An Ecological Approach	T. C. Emmel, Univ. Florida
	7 Land & Life in the Tropics	J. J. Parsons, Univ. Calif. Berkeley
	8 Field Dendrology	J. S. Bethel, Univ. Washington
1969	1 Tropical Biology: An Ecological Approach	N. J. Scott, Univ. Connecticut
	2 Principles of Tropical Grassland Ecology	D. E. McCloud, Univ. Florida
	3 Introduction of Tropical Forestry	F. D. Johnson, Univ. Idaho
	4 Tropical Biology: An Ecological Approach	N. J. Scott, Univ. Connecticut
	5 Tropical Biology: An Ecological Approach	R. J. Goodland, McGill Univ.
	6 Advanced Population Biology	D. H. Janzen, Univ. Chicago G. H. Orians, Univ. Washington
	7 Tropical Marine Biology	G. J. Bakus, Natl. Acad. Sciences P. W. Frank, Univ. Oregon

APPENDIX 1 (Continued)

1970	1	Tropical Biology: An Ecological Approach	N. J. Scott, Univ. Connecticut
	2	Tropical Limnology	D. G. Frey, Indiana Univ. E. S. Deevey, Dalhousie Univ.
	4	Regional & Economic Geography of Guatemala	S. B. Bonis, Inst. Geogr. Nac. Guatemala
	5	Field Course in the Geography of Costa Rica	C. L. Johannessen, Univ. Oregon
	6	Tropical Forestry	H. Riekerk, Univ. Washington
	7	Tropical Biology: An Ecological Approach	N. J. Scott, Univ. Connecticut
	8	Tropical Biology: An Ecological Approach	M. E. Mathias, UCLA T. E. Moore, Univ. Michigan
	9	Atmospheric Sciences	J. F. Griffiths, Texas A&M Univ.
	10	Tropical Marine Biology	G. J. Bakus, Natl. Acad. Sciences
1971	1	Tropical Biology: An Ecological Approach	R. K. Colwell, Univ. Calif., Berkeley
	2	Habitat Exploitation & Diversity: An Ecological Approach w/Vertebrates	R. W. McDiarmid, Univ. So. Florida
	3	Tropical Forestry	H. Riekerk, Univ. Washington
	4	Recent Carbonate Sedimentation and Early Diagenetic Process	C. H. Moore, Louisiana State Univ.
	5	Tropical Biology: An Ecological Approach	J. H. Vandermeer, Univ. Michigan
	6	Tropical Biology: An Ecological Approach	E. G. Farnworth, Univ. Florida
	7	Physical Landscape & Settlement Patterns	O. H. Horst, Western Michigan Univ.
	8	Atmospheric Energy Considerations in a Tropical Environment	J. F. Griffiths, Texas A&M Univ.
1972	1	Tropical Biology: An Ecological Approach	O. R. Taylor, Univ. Kansas
	2	Advanced Biology: Central American Pine Forests, Temperate "Islands" in a "Sea" of Tropical Vegetation	G. H. Orians, Univ. Washington
	3	Tropical Biology: An Ecological Approach	D. E. Gill, Univ. Maryland
	4	Geography: Man's Impact on Tropical Forest Ecosystems in Costa Rica, Past & Present	R. C. West, Louisiana State Univ.
1973	1	Tropical Biology: An Ecological Approach	O. R. Taylor, Univ. Kansas
	2	Tropical Biology: An Ecological Approach	M. F. Willson, Univ. Illinois C. E. Schnell, Johns Hopkins Univ.
1974	1	Tropical Biology: An Ecological Approach	C. R. Carroll, SUNY, Stony Brook
	2	Ecología de Poblaciones	F. G. Stiles, D. C. Robinson, and S. Salas, Univ. Costa Rica
	3	Tropical Biology: An Ecological Approach	D. E. Wilson, U. S. Fish & Wildlife
	4	Coral Reef Ecology	C. H. Moore, Louisiana State Univ.
1975	1	Ecología de Poblaciones	F. G. Stiles, Univ. Costa Rica
	2	Tropical Biology: An Ecological Approach	J. J. Ewel, Univ. Florida
	3	Tropical Parasitology	D. Pence, Texas Tech Univ.
1976	1	Ecología de Poblaciones	D. C. Robinson, Univ. Costa Rica
	2	Tropical Biology: An Ecological Approach	H. A. Hespenheide, UCLA

APPENDIX 1 (Continued)

1977	2 Ecología Marina	M. M. Murillo, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	D. R. Strong, Florida State Univ.
	4 Tropical Biology: An Ecological Approach	E. W. Stiles, Rutgers Univ.
1978	1 Tropical Biology: An Ecological Approach	G. S. Hartshorn, Tropical Sci. Ctr.
	2 Ecología de Aracnidos	C. E. Valerio, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	D. P. Janos, Smithsonian Tropical Research Institute
1979	1 Tropical Biology: An Ecological Approach	B. L. Bentley, SUNY, Stony Brook
	2 Ecología de Poblaciones	F. G. Stiles, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	D. E. Gill, Univ. Maryland
1980	1 Tropical Biology: An Ecological Approach	R. J. Stout, Michigan State Univ.
	2 Ecología de Poblaciones	W. R. Soto, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	L. A. Real, No. Carolina State Univ. J. Lanza, Bethany College
1981	1 Tropical Biology: An Ecological Approach	M. V. Price & N. M. Waser, Univ. Calif., Riverside J. C. Schultz, Dartmouth College
	2 Ecología de Poblaciones	W. R. Soto, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	G. W. Otis, Univ. Guelph
1982	1 Tropical Biology: An Ecological Approach	G. B. Williamson, Univ. Miami
	3 Tropical Biology: An Ecological Approach	J. M. Wunderle, Jr., Univ. Puerto Rico, Cayey
1983	1 Tropical Biology: An Ecological Approach	C. M. Simon, Univ. Hawaii R. J. Stout, Michigan State Univ.
	3 Tropical Biology: An Ecological Approach	R. G. Zahary, CSU, Los Angeles
1984	1 Tropical Biology: An Ecological Approach	D. J. Futuyma, SUNY, Stony Brook
	3 Tropical Biology: An Ecological Approach	W. A. Haber, Univ. Calif., Berkeley
1985	1 Tropical Biology: An Ecological Approach	J. S. Denslow, New York Botanical Garden
	2 Ecología de Poblaciones	F. G. Stiles, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	R. J. Marquis, Univ. Illinois
	4 Tropical Agricultural Ecology	S. R. Gliessman, Univ. California, Santa Cruz
1986	1 Tropical Biology: An Ecological Approach	F. E. Putz, Univ. Florida
	2 Ecología de Poblaciones	F. G. Stiles, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	C. K. Augspurger, Univ. Illinois
	4 Tropical AgroEcology	M. E. Swisher, Univ. Florida

APPENDIX 1 (Continued)

1987	1 Tropical Ecology: An Ecological Approach	R. J. Stout, Michigan State Univ. C. R. Carroll, Univ. Calif. Nat. Reserves
	2 Ecología de Poblaciones	F. G. Stiles, Univ. Costa Rica
	3 Tropical Biology: An Ecological Approach	H. E. Braker, Univ. Calif., Riverside D. H. Feener, Smithsonian Tropical Research Institute E. W. Schupp, Univ. Iowa
	4 Tropical Agricultural Ecology	D. H. Boucher, Univ. Québec, Montréal C. Staver, Cornell Univ.
	5 Agroforestry	G. S. Hartshorn, Tropical Science Center R. F. Fisher, Utah State Univ.

TROPICAL RAINFOREST ECOLOGY FROM A CANOPY PERSPECTIVE

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Many processes that are fundamental to tropical rainforest maintenance and regeneration take place in the forest canopy. Recently developed access techniques afford biologists non-destructive means to document and quantify canopy biota and their accompanying activities and interactions. Results from studies involving within-canopy observations and measurements of nutrient cycling, epiphyte distribution, species diversity, nutrient cycling, and animal activities in primary and secondary forest are reviewed to identify specific areas of investigation and scientific questions that can be addressed from a canopy perspective. The ongoing progress of current canopy ecology projects in tropical rainforests is described. New data on interactions between neotropical canopy birds and plants and the effects of forest conversion to pasture on these organisms in a neotropical cloud forest suggest that trees left standing in pastures can serve as "island refuges" for a wide variety of bird species using canopy resources such as epiphyte flowers and fruits and accumulated dead organic matter on branches and trunks. This study points out the need for more basic ecological research on canopy ecology in both primary and converted forests.

For those concerned with the ecology and conservation of the diverse genetic and ecological resources of tropical rainforests, studies in the upper tree canopy of rainforests are of fundamental importance. In the treetop region of tropical forests, abundant energy and distinctive microclimatic regimes foster up to 40% of the earth's inventory of species (Perry 1984). Until recently, the canopy has been a largely inaccessible and unexplored area of tropical forests. Indeed, those who did venture into the canopy have been regarded by the scientific community as "Tarzan types" who have had little to contribute outside of providing rarely collected specimens and interesting

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natural history stories. Recent applications of safe and reliable mountain-climbing techniques for routine and extended access into tropical rainforest tree crowns, however, have expanded the range of questions ecologists can pose that bear upon basic and applied aspects of tropical forest ecology. The upper tree canopy is being recognized as an appropriate arena to investigate such ecological questions as the evolution of symbiotic interactions, mechanisms of nutrient conservation, and comparative studies of life histories of canopy-dwelling plants and their associated animal pollinators and dispersers.

A growing body of ecological research indicates that processes occurring in this region of the forest relate directly to the overall composition, function and dynamics of rainforests as a whole. This study addresses the following areas of canopy ecology pertinent to tropical rainforest research:

(1) overall attributes of canopy microclimate;

(2) methods that have been developed for access to the canopy;

(3) some of the questions that can be addressed from the canopy perspective and specific examples of studies addressing such questions; and

(4) new data on the interactions of canopy-dwelling plant and bird communities in a neotropical cloud forest and some of the effects of forest conversion to various types of pasture on these interactions.

THE CANOPY AND ITS MICROCLIMATE

The term "canopy" is generally used to denote "any high overarching covering." More specifically, it defines the upper portion of a single tree crown and/or the entire upper portion of forest ecosystems. In earlier accounts, tropical rainforests were perceived as being strongly stratified into discrete, multiple layers (Aubréville 1965, Richards 1952), with the canopy encompassing the crowns of the emergent trees ("A" horizon) and the contiguous "B" horizon (Richards 1952, Whitmore 1975). This level of the forest may be contiguous or "broken" in horizontal space (Hallé et al. 1978, Richards 1983).

The complex three-dimensional structure of tropical rainforests has stimulated the documentation of physiognomy and vertical stratification of abiotic and biotic attributes of the forest as a whole (Hallé et al. 1978). Stratification of microclimatic regimes and the composition and distribution of the biota are striking, especially in humid lowland forests (Longman and Jeník 1974). Canopy microclimatology has been measured most frequently with instruments mounted on towers at various heights above the forest floor (e.g. Bunning 1948, Carter 1934). Since above-canopy conditions closely resemble those recorded in openings in forest gaps, some studies have directly compared ground measurements of the forest interior with measurements collected at clearings in the forest (Allee 1926, Schulz 1960). More recently,

the use of battery-powered data-loggers has provided continuous monitoring of environmental conditions, with sensors installed at a range of canopy heights (e.g. Chazdon and Fetcher 1984).

In general, canopy abiotic conditions are typified by more intense sunlight, greater extremes of relative humidity, higher water stress, and a smaller, more pulse-supplied pool of nutrients than forest floor conditions (Kira et al. 1969, Lee 1978, Yoda 1974, Benzing 1981a). Sunlight attenuation, for example, can be as great as 98% between the tops of emergent trees and the levels reaching the forest floor (Cachan 1963). Rates of evaporation in the canopy have been recorded that are comparable to those occurring in open savannas. Relative humidity can range from nearly 100% at night to less than 30% during the midday in the dry season (Jeník and Hall 1966). Differences in canopy vs. forest floor wind speeds are most extreme in montane cloud forests. In a Costa Rican ridge cloud forest, Lawton (1980) clocked wind speeds within the canopy (8 m) at 11.3 m/s, while forest floor (2 m) speeds were only 4.0 m/s.

CANOPY ACCESS TECHNIQUES

The biota of the upper tree canopy has attracted attention ever since the first European explorers traveled to tropical latitudes. However, the techniques required for the study of canopy communities have become available only recently. Pioneering work in old-growth forests of the Pacific Northwest, United States by Denison et al. (1972) led to the application of mountain-climbing techniques for safe and reliable access to the canopies of tall trees. These techniques were modified for use in the tropics by Perry (1978, 1984) and others (Nadkarni 1983, Whitacre 1981).

Mitchell (1982) provides an excellent summary of methods of canopy access. He organized the existing techniques into six categories:

(1) construction of permanent towers (e.g. Grison 1978, Haddow 1961);

(2) ascension of the trunk with bolts, spikes, or ladders (Hingston 1932; Denison et al. 1972, Denison 1973);

(3) construction of platforms within tree crowns (McClure 1966, Sutton 1983), and installation of rope webs (Perry 1984);

(4) construction of aerial walkways (Dieterlien 1979, Mitchell 1982);

(5) "miscellaneous methods" such as the use of hot air balloons, helicopters, and hang-gliders (Hladik and Hladik 1980); and

(6) climbing free of the trunk, using single-rope techniques (SRT) (Perry 1978, Whitacre 1981).

SRT techniques are appropriate to collect many types of ecological data in the canopy. They are non-destructive to the tree, relatively inexpensive, rapidly installed, and easily learned. SRT techniques also minimize contact

with tropical tree trunks, their potentially irritating spines, and animals. This method provides maximum flexibility, as it requires a minimum of one strong branch within shooting range of a powerful slingshot, crossbow, or linegun.

This climbing process proceeds in the stages outlined in Figure 1. First, a climbing rope is placed over a suitable branch or branches by shooting a mono-filament nylon line over it with a crossbow or "master-caster." The latter consists of a powerful slingshot mounted on the side of a short aluminum rod (50 cm), with a spinning reel mounted beneath it (Nadkarni 1983). A nylon "parachute" cord is then attached and pulled over the branch with the reel. This is followed by pulling up a standard (9 or 11 mm) climbing rope, which is tied off to the trunk. The climber then ascends the rope with a seat harness, leg loops, and "Jumar" type self-locking ascenders. The climber can rest or take samples and abiotic measurements on the journey up the rope. By shooting lines from one limb to another, one can "leap-frog" to other trees across the canopy. The return to the ground is accomplished by reversing the ascension process or by rappelling down with brake bars.

Equipment for these techniques (approximately US $300) is readily available at outdoor equipment stores. It can be carried in a single backpack. Trees can be rigged in 30 minutes and climbed to 30 m in 5 to 10 minutes. The intermediate nylon line can be left in a tree for rapid re-rigging.

AREAS OF CANOPY ECOLOGICAL RESEARCH

A number of biological questions can be addressed from the canopy perspective, ranging from basic taxonomic studies of canopy-dwelling organisms to applied studies of nutrient cycling and productivity. Canopy studies have enhanced our general understanding of tropical forest ecology in these areas:

(1) tropical forest nutrient cycling, especially with regard to identification of mechanisms of nutrient conservation;

(2) documentation of the overall species diversity of tropical systems;

(3) biotic and abiotic factors controlling plant distribution and abundance;

(4) attributes and evolution of such plant-animal interactions as herbivory, pollination, and fruit dispersal; and

(5) effects of disturbance on natural communities.

Nutrient Cycling

Nutrient cycling within the canopy has recently attracted a good deal of attention. It has been extensively reviewed elsewhere (Benzing 1983, Nadkarni 1984, 1985, 1986). In the last decade, ecosystem-level studies have identified the forest canopy as having important storage and regulatory roles

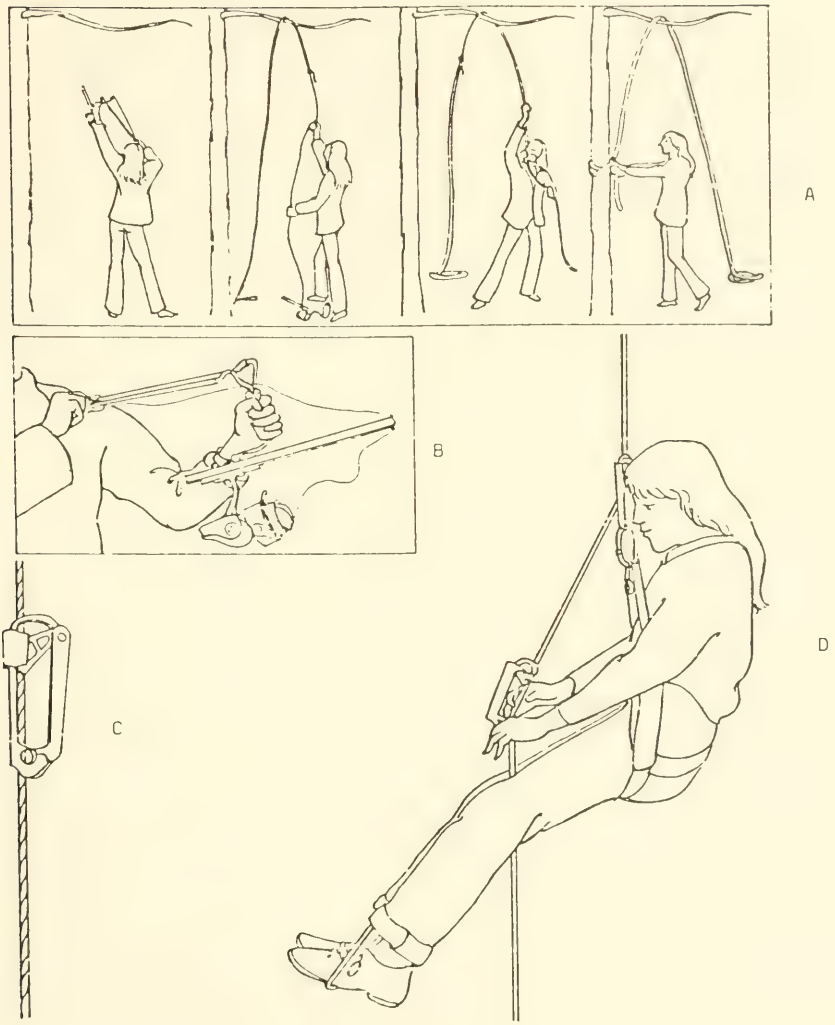

Fig. 1. Sequence of tree-climbing protocol using single-rope technique described in text. A. Tree-rigging sequence. B. "Master-caster" device for placement of initial line. C. "Jumar" ascender clamp attached to seat harness and leg loops. D. Climbing harness and leg loops.

in overall mineral cycling. In contrast to the traditional paradigm of temperate forest nutrient cycling, in which the bulk of the nutrient pool is stored in the forest floor and soil, there is growing recognition that forest fertility in some sites is largely a function of mechanisms within the biotic components of the ecosystem (Jones et al. 1974, Kellman et al. 1982, Golley 1983, Vitousek 1984). Intact forests possessing these mechanisms are characterized by large nutrient fluxes within the biota relative to ecosystem loss. Mechanisms of nutrient conservation are ultimately explained by the living organisms that make up the forest community, especially at the soil-litter-root interface. As one of the constituents of the biotic component of wet forests, canopy-held organic matter may play an important regulatory role in nutrient storage and flux.

Evidence that the canopy subsystem is important in overall nutrient cycling comes from five lines of evidence:

(1) large nutrient pools are contained in live and dead decomposing organic matter within the canopy (Pócs 1980, Nadkarni 1983);

(2) tree canopy structure increases the interception of airborne nutrients in rain, mist, rime, and dust (Weaver 1972, Azevedo and Morgan 1974, Cronan and Reiners 1983);

(3) activities of free-living and symbiotic organisms can biologically fix significant amounts of atmospheric nitrogen (Denison 1973, Roskowski 1980, Sengupta et al. 1981, Yatazawa et al. 1983, Bentley and Carpenter 1984);

(4) active absorptive organs exist within tree crowns, including tree stems (Ticknor 1953), foliar surfaces (Thorne 1955), and host tree canopy root systems (Nadkarni 1981);

(5) many canopy-dwelling plants are morphologically and physiologically efficient at impounding pulse-supplied nutrients and tying them into the biotic portion of the system, which can reduce loss to the system as a whole (Benzing 1983).

In only a few studies, however, has nutrient flux within the canopy been directly measured (e.g. Edminsten 1970, Pike 1971, Nadkarni 1983). No one has attempted to quantify or compare the nutrient dynamics within the canopy with that of the forest overall nutrient cycles. Yet this direct comparison is crucial if we are to determine the importance of different parts of an ecosystem in its overall functioning and to predict the effects of canopy disturbance.

Laboratory studies using newly developed techniques of gamma spectrometry have been carried out to determine the rates and fates of nutrients delivered to canopy vs. below-ground absorptive surfaces (Nadkarni and Primack, in prep.). Above-ground canopy roots of willow saplings, for instance,

are capable of nutrient uptake and circulation of radioactive tracers at rates comparable to those in soil roots, indicating that nutrient cycling within the crowns of epiphyte-laden trees may be significant in the field.

In addition to their probable importance in overall nutrient cycles of natural forests, canopy components have high potential for increasing our understanding of mechanisms regulating nutrient storage and transfer. The epiphyte-organic matter-host tree systems create "natural microcosms" and are excellent arenas for investigating processes of mineral circulation. Unlike laboratory microcosms using columns of sand or water culture, these systems contain all the components that "real" ecosystems have (humus, vascular and non-vascular plants, a substrate) and have occurred in nature over an evolutionary time scale. They can be subjected to controlled and replicated manipulations; nutrient inputs and outputs can be monitored accurately. Undoubtedly this could develop into a fruitful area of nutrient cycling research.

Species Diversity of Canopy Biota

Among the most striking and unique attributes of tropical rainforest canopies are the diversity and abundance of the plant communities that are physically independent of the forest floor for all or part of their life cycle. The species diversity of epiphytes, plants which derive support but not nutrients from their hosts (Abercrombie et al. 1970), has been recently reviewed by Madison (1977) and Gentry and Dodson (1987). They belong to a wide range of vascular and non-vascular plant taxa. Sixty-eight vascular plant families contain epiphytic members; 28,624 species are epiphytic, which comprise about 13% of the total vascular flora. A large number of non-vascular plants, many as yet unnamed, are also abundant in tropical forests, and in fact dominate (by biomass) the epiphyte communities of some neotropical cloud forests and temperate moist forests (Nadkarni 1984, 1985).

Various ecological and taxonomic aspects of other types of canopy plants have been documented. These include parasites (Davidar 1983, Calder and Bernhardt 1983), lianas (Putz 1982), and epiphylls (Bien 1982, Bentley and Carpenter 1984). However, the full scope of their contribution to overall tropical forest species diversity remains unknown.

A body of research concerns the diversity of canopy-dwelling animals (e.g. McClure 1966, Sutton 1983, Sutton et al. in press, Sutton and Hudson 1980). Most of the research has concerned insects and other arthropods. Landmark studies by Erwin (1982), which focused on the diversity of specific groups of beetles, pointed out that overall estimates of species diversity in the tropics are gross underestimates if the diversity of canopy organisms is not included. Use of remote-controlled insecticidal foggers following Gagné (1979) and Gagné and Martin (1979) resulted in an estimate of the total

number of individuals and the degree of host-specificity for a number of insect groups. Erwin (1983) reported 1000 species of beetles (excluding weevils) on a single tree, and 12,448 per ha of forest canopy in Manaus, Brazil. Relating his assessment of the numbers of host-specific species to other arthropods, the estimate of arthropod diversity was 41,389 spp/ha, and overall, 30 million species of tropical arthropods. These studies are an important first step in accurately assessing tropical rainforest diversity.

Biotic Influences on Epiphyte Distribution and Abundance

The biotic factors regulating where and how many plants grow in a given area are a central question for plant ecologists (Grieg-Smith 1983). The variations of within- and between-tree epiphyte distributions present an appropriate arena to test theories on the regulatory factors that control plant distributions. Questions concerning host tree specificity, within-canopy stratification, and mechanisms whereby host trees may affect epiphyte establishment have intrigued botanists for many years (e.g. Went 1940, Barkman 1958). The mechanisms for host tree specificity remain poorly understood, although many have speculated that bark texture and pH, bark and branch shedding rates, and chemical exudates may facilitate or inhibit epiphyte colonization and growth. The few experimental studies have been carried out mainly in the subtropics and temperate regions (e.g. Frei and Dodson 1972, Benzing 1978, 1981b, Schlesinger and Marks 1977).

Descriptive and qualitative studies of epiphyte distributions have been used primarily to make inferences about regulation of epiphyte growth by the host tree. The most exhaustive studies of epiphyte distributions within tropical forests have been based on visual inventories. Various authors concluded that for many species, there is some degree of host tree specificity (Went 1940, Johansson 1974, Sugden and Robins 1979). A more focused study carried out in the lowland forests of Malaysia by Johnson and Awan (1972) compared differences in abundance, biomass, and accumulated organic matter between epiphytes growing on *Fagraea fragrans* and *Swietenia macrophylla*. Their results showed that several of the epiphytes were host-specific (e.g. *Pyrrosia angustata, Platycerium coronarium* only on *F. fragrans, Phymatodes scolopendria* and *Drynaria sparsisora* only on *S. macrophylla*), while others (*Asplenium nidus*) did not show such host tree preferences. No experimental evidence for causes of these patterns was presented.

Plant/Animal Interactions in the Canopy

A wide range of plant-animal interactions that are fundamental to the reproductive apparatus of the forest occur within the upper tree canopy.

These interactions have been documented mainly from plant collection notes and anecdotal observations, and include canopy herbivory, ant/epiphyte relationships (Huxley 1980, Longino 1986, Madison 1979), and fruit and seed dispersal of canopy trees (Wheelwright et al. 1984). Special attention has been given to reproductive biology of bromeliads (Benzing 1980) and orchids (Dressler 1981). Studies on the highly specific relationships between hummingbirds and epiphytic ericaceous shrubs indicate that morphological and behavioral specialization may function to allow coexistence of diverse species complexes (Feinsinger et al. 1986).

Most of the work on bird frugivory in tropical forest canopies (Snow 1981) has focused on the consumption of fruits of canopy trees with respect to tree dispersal and/or avian nutrient budgets (e.g. Wheelwright et al. 1984). In many tropical forests, the epiphyte community provides energy, nutrients, water, and nesting materials from their foliage, flowers, fruits, accumulated dead organic matter, and rosette pools to canopy-dwelling animals. A recent study (Nadkarni and Matelson, in prep.) was conducted to provide a framework to understand the degree of dependency of particular animals upon various resources held within the canopy, with a focus on bird use of epiphytes.

Epiphyte distribution and bird visitation were monitored in an area of lower montane cloud forest and adjacent pastures in Monteverde, Costa Rica (Fig. 2) from June 29–September 6, 1985. Using SRT techniques previously described, we established canopy perches (hanging collapsible cots) in dominant canopy trees located in primary leeward cloud forest. Bird activities could be accurately seen in tree crowns within a radius of 120 m from the perches (8 to 14 individuals in each of three sites) (Fig. 3). Observation sessions (four 90-minute sessions per day) were timed to occur throughout the day (0600 to 1800) in order to control for diurnal variations in bird visitation. During the 775 hours of observations, we recorded the number of individual bird visits, species, length of visit, behavior (perching, foraging, feeding, nesting, mating, vocalizing), and canopy resource used (epiphyte, host tree, flower, fruit, water, invertebrate, nesting material).

We found that epiphytes provide many birds with habitat and supplies of energy and nutrients. In this preliminary analysis, the most commonly used resource plants were clustered in major family or generic groupings, which provide specific resources presented in Table 1. Resource availability presented here represents conditions that occur during the middle of the wet season (June to September), and vary to an unknown extent, depending on the phenology of the epiphytes and host trees, seasonal changes in weather, and successional changes and disturbances within the epiphyte community.

Epiphyte resources were used by 46 of the total 86 bird species that used

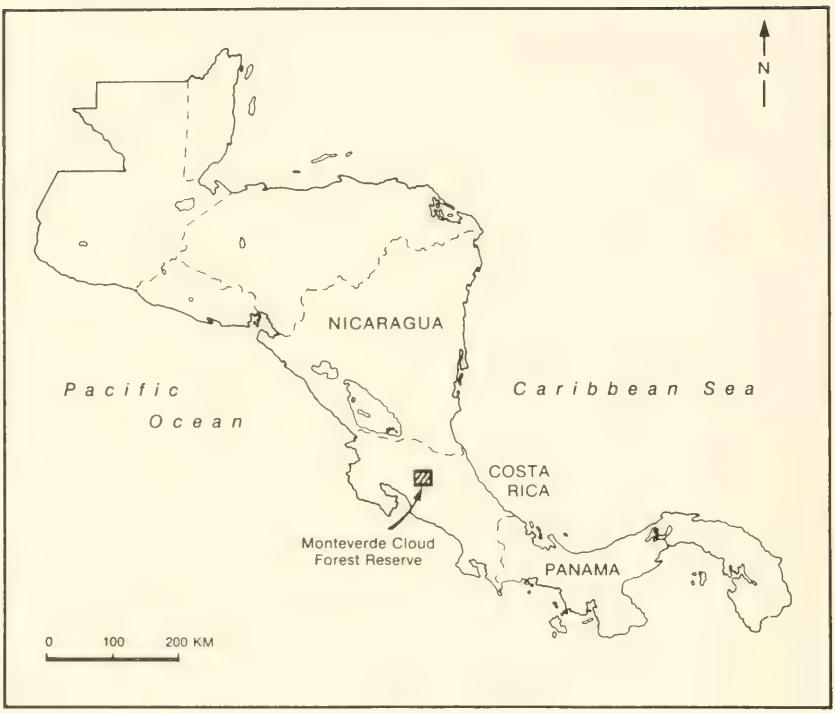

Fig. 2. Location of Monteverde cloud forest.

TABLE 1. EPIPHYTE TYPE AND RESOURCES AVAILABLE FOR CANOPY BIRD USE

Epiphyte Resource	Epiphyte Type†				
	A	B	E	M	L
Inflorescence	*	*	*		
Fruit	*	*	*		
Invertebrates		*	*	*	
Water		*			
Nesting Material				*	*

† A = Aroids; B = Bromeliads; E = Ericaceous shrubs; M = Mosses and liverworts; L = Lichens.

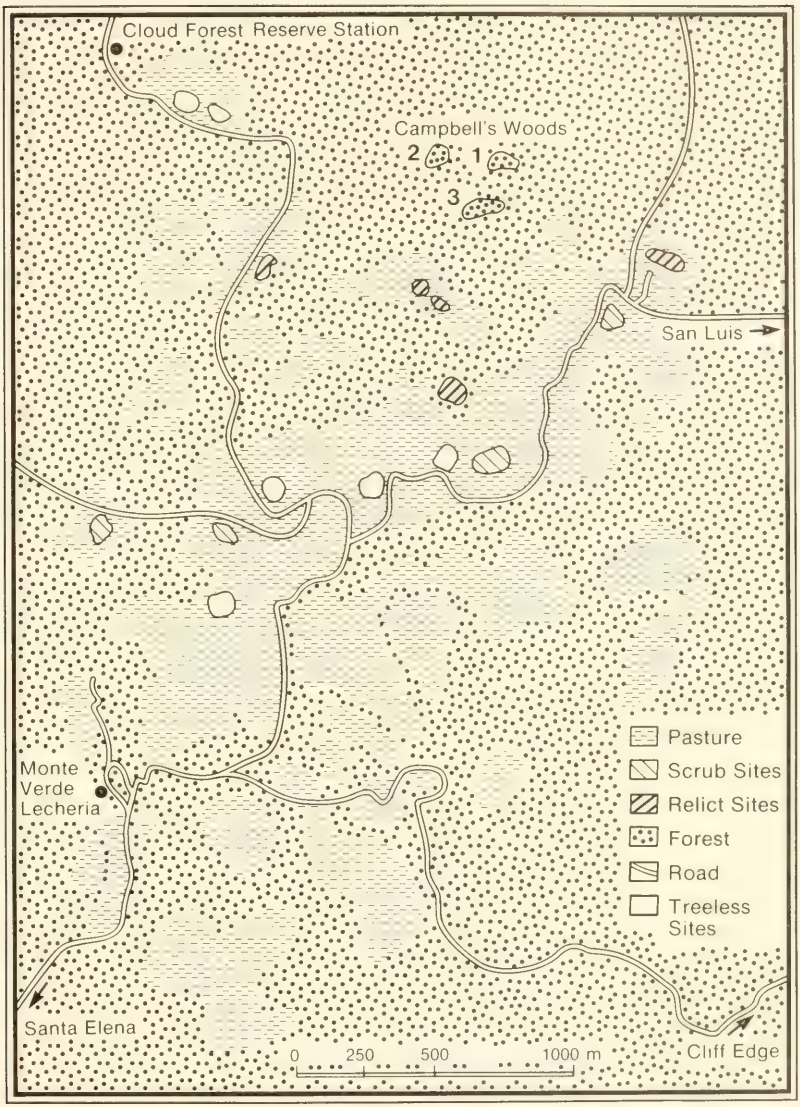

Fig. 3. Detailed map of study sites for bird use of tree crowns in forest and pasture areas, Monteverde, Costa Rica. Numbered plots are those used for canopy observations in primary forest. Relict pastures are those where original rainforest trees have been left standing. Scrub pastures are those colonized by a limited number of "invader" tree species. Map drawn from an aerial photograph by Instituto Metorológico, San José, Costa Rica, 1979.

our sites. Mosses and associated dead organic matter were used by the greatest number of bird species, followed by ericaceous shrubs and bromeliads (Table 2). Forty-eight percent of the bird species used only one epiphyte type, but three (Common Bush Tanager, Southern House Wren, and Scarlet-thighed Dacnis) were generalists on all epiphyte types. This indicates that epiphytes in primary forest tree canopies provide potentially important food, water, and habitat resources for the avian community, but further work is needed to determine the degree of bird dependence on canopy-dwelling plants.

THE EFFECTS OF FOREST CONVERSION ON CANOPY BIOTA

In addition to basic ecological questions on canopy biota in primary forests, there is much to be learned about canopy communities of secondary forests and in trees growing in land that has been converted to pasture. Little work has been done in this area. However, the increasing extension and intensity of deforestation has been well documented elsewhere (e.g. Lovejoy and Oren 1981) and is attracting worldwide attention. What is urgently needed is scientific information on the effects of forest conversion on different parts of primary and modified ecosystems in order to understand and potentially mitigate negative effects.

One of these questions is to understand the patterns and processes that occur in the crowns of trees that grow in pastures following conversion of forests. Pasture trees can differ greatly in species composition, architecture, and in the biotic characteristics that potentially determine canopy microclimate and plant and animal communities. Although this has never been directly quantified, epiphyte loads differ considerably in both composition and abundance between primary and secondary forests. As with other island communities (Wilcox and Murphy 1985), the isolation of "island" trees in a sea of pasture may result in changes that affect canopy-dwelling biota in a variety of ways; canopy organisms may be positively, negatively, or not at all affected by these differences.

Conversion of forest can result in several pasture tree types. In some cases, farmers leave standing a small number of "relict" trees, i.e. trees of the original forest, creating so-called "relict pastures." Epiphyte loads within the upper tree crown appear to remain relatively intact for a number of years, though trunk epiphytes found on their forest interior conspecifics are often absent (N. Nadkarni, pers. obs.). In other cases, all of the original trees are removed, and only "scrub trees" capable of invading and maintaining themselves in pastures occur ("scrub pastures"). These weedy trees are typically short in stature, fast-growing, with open crowns. Their epiphyte loads are usually of smaller biomass and lower species diversity than similarly sized trees in primary forest or in relict pasture trees (Nadkarni, pers. obs.).

TABLE 2. CANOPY BIRD USE OF EPIPHYTE RESOURCES IN MONTEVERDE, COSTA RICA

BIRD Common Name	Scientific Name	EPIPHYTE RESOURCE*				
Fork-tailed Woodnymph	*Thalurania furcata*			E		
Stripe-tailed Hummingbird	*Eupherusa eximia*			E		
Coppery-headed Hummingbird	*Elvira cupreiceps*			E		
Purple-throated Mountaingem	*Lampornis calolaema*			E	M	
Green-crowned Brilliant	*Heliodoxa jacula*			E	M	
Prong-billed Barbet	*Semnornis frantzii*	A			M	
Rufous-collared Sparrow	*Zonotrichia capensis*			E		
Spotted Barbtail	*Premnoplex brunnescens*				M	
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*			E		
Golden-bellied Flycatcher	*M. hemichrysus*		B			
Boat-billed Flycatcher	*Megarhynchus pitangua*		B		M	
Dusky-capped Flycatcher	*Myiarchus tuberculifer*		B			
Yellow-bellied Elaenia	*Elaenia flavogaster*			E		
Mountain Elaenia	*E. frantzii*				M	
Paltry Tyrannulet	*Tyranniscus vilissimus*				M	
Olive-striped Flycatcher	*Mionectes olivaceus*				M	
Brown Jay	*Psilhorinus morio*		B			
Southern House Wren	*Troglodytes musculus*		B	E	M	L
Ochraceous Wren	*T. ochraceus*		B		M	
Clay-colored Robin	*Turdus grayi*		B		M	
Mountain Robin	*T. plebejus*		B		M	
Black-faced Solitaire	*Myadestes melanops*	A			M	
Brown-capped Vireo	*Vireo leucophrys*				M	
Scarlet-thighed Dacnis	*Dacnis venusta*		B	E	M	
Bananaquit	*Coereba flaveola*			E		
Black and White Warbler	*Mniotilta varia*				M	
Slate-throated Redstart	*Myioborus miniatus*				M	
Three-stripe Warbler	*Basileuterus tristriatus*				M	
Blue-crowned Chlorophonia	*Chlorophonia occipitalis*			E	M	
Yellow-throated Euphonia	*Euphonia hirundinacea*			E	M	
Blue-gray Tanager	*Thraupis episcopus*			E	M	
Hepatic Tanager	*Piranga flava*		B		M	
Common Bush Tanager	*Chlorospingus ophthalmicus*		B	E	M	L
Yellow-throated Brush-Finch	*Atlapetes gutturalis*			E	M	
Red-faced Spinetail	*Cranioleuca erythrops*		B		M	

* A = Aroids; B = Bromeliads; E = Ericaceous shrubs; M = Mosses and liverworts; L = Lichens. Bird names follow Slud (1964) and Ridgely (1976).

One effect of the conversion of primary forest pastures on canopy communities could be reflected in differences in bird use of epiphytes between crowns of trees located in primary forest, relict pasture, and scrub pasture. The study on epiphyte/bird interactions described above also encompassed the question of these interactions in different habitat types (Nadkarni, in prep.). Thirteen study sites (150 x 150 m) were located in primary forest, relict pastures, and scrub pastures within the mosaic of habitat and land use history, determined by information from local farmers of Monteverde (Fig. 3). Bird use of epiphytes was monitored during the same study period and on the same schedule as described above. Observations of bird visitation and bird use of epiphytes were taken simultaneously by three observers at three different sites to allow for direct comparison of these activities.

The number of bird species using various epiphyte resources in each habitat during the study period is presented in Figure 4. The groups were lumped as follows: bromeliads; ericaceous shrubs; *Norantea* sp. (a fruiting epiphytic shrub, Marcgraviaceae); *Lycianthes* sp. (a fruiting epiphytic shrub, Solanaceae), and dead organic matter that accumulates beneath mats of mosses and liverworts. These data indicate that epiphytes on trees growing in pastures are visited by a high diversity of bird species. A surprisingly large

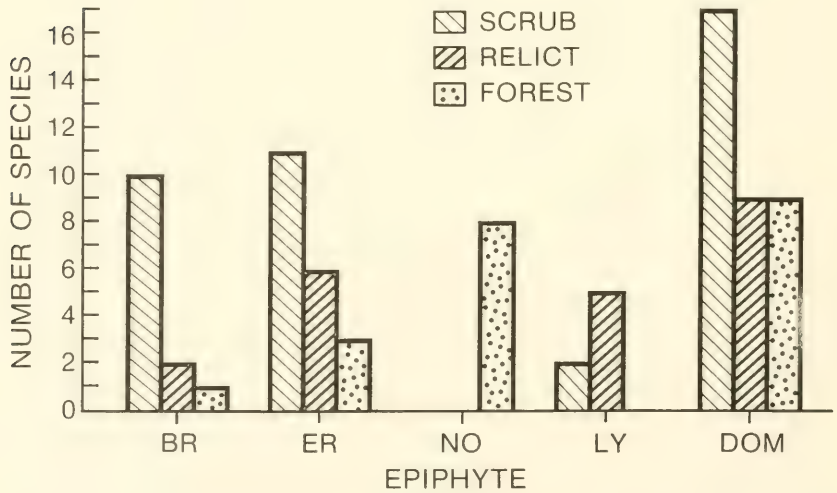

Fig. 4. Total number of bird species using epiphytes in forest, relict pasture, and scrub pasture study sites, June 29 – September 5, 1985. BR = bromeliads; ER = ericaceous shrubs; NO = *Norantea* sp.; LY = *Lycianthes* sp.; DOM = Dead Organic Matter.

number of bird species utilized epiphytes on scrub trees; in the case of bromeliads, ericads, and dead organic matter, scrub pasture trees provided a greater diversity of birds with resources. This preliminary information suggests that trees left standing in pastures and those invading following forest conversion provide canopy-held resources that are accessible to a large number of tropical bird species.

This study is a first step in comparing canopy communities in primary forest trees and in trees located in habitats that have been altered following timber or forage production. Future research should focus on: (a) seasonal dynamics of bird canopy use, (b) migrant vs. resident bird use of canopy resources, and (c) the relationship between epiphyte vs. host tree resource abundance and availability in a wide variety of land use and habitat types.

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THE SEARCH FOR SOLUTIONS: RESEARCH AND EDUCATION AT THE LA SELVA BIOLOGICAL STATION AND THEIR RELATION TO ECODEVELOPMENT

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The history and development of the La Selva Biological Station in Costa Rica are reviewed. La Selva is the principal field station of the Organization for Tropical Studies, an international consortium of more than forty universities and museums, with the primary mission of encouraging research and teaching in tropical biology.

Tropical deforestation and the maintenance of tropical biological diversity are serious global issues. Much of the research carried out at La Selva is directly or indirectly contributing solutions to these problems. La Selva is also a center for teaching tropical biology to a diverse array of students, from school children of the community to graduate-level biologists from many countries.

Biological stations in the tropics can contribute in important ways to ecodevelopment. The La Selva synergism of research, teaching, ecotourism, and a broad base of institutional support offers one model for the development of a tropical biological station.

Tropical rainforests, the world's greatest storehouse of biological diversity, are disappearing at an alarming rate throughout the world (Myers 1983a). Various authors have written eloquently about the rates, causes, and consequences of this process (e.g. Myers 1979, 1980, 1983b, 1984; Iltis 1983). I present a different perspective of tropical deforestation and what can be done about it. In contrast to a global view of deforestation, I will concentrate on one particular area in the lowland tropics of Costa Rica, Central America. For the past six years I have lived and worked at the La Selva Biological Station, which is located on a frontier between virgin rainforest and an advancing

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front of deforestation. From this viewpoint I will describe the history of deforestation and the forces driving the process in this region. The biological research under way at La Selva can have far-reaching impacts on development, and I will show how research in many different disciplines is directly or indirectly providing data needed for rational long-term land management. Tropical biological field stations everywhere are now or soon will be facing similar pressure and opportunities.

THE LA SELVA BIOLOGICAL STATION

The La Selva Biological Station, located in the Atlantic lowlands of Costa Rica, Central America (Fig. 1), is a world center for tropical rainforest research. Since 1968 the station has been operated by the Organization for Tropical Studies (OTS), an international consortium of universities and museums dedicated to research and education in tropical biology (Stone, this volume). OTS seeks to carry out these goals at La Selva by providing logistical support to visiting scientists and courses.

The station encompasses 1500 ha, and includes a wide variety of terrestrial and aquatic habitats. In addition, La Selva borders an area of ca. 45,000 ha of protected forest (Pringle, this volume). Besides this range of tropical habitats, station users have access to laboratory facilities, vehicles and boats, field assistants, contacts to Costa Rican researchers and students, and administrative support for purchasing and logistic needs.

OTS has traditionally viewed itself as facilitating tropical research, not actually carrying out investigations. The current staff of the station reflects this orientation; of 32 employees, only the Co-Directors and the Assistant Director are scientists. Due to the OTS policy of accepting all ecologically compatible research projects, the work done at La Selva to date has reflected the particular interests of scientists and funding agencies. In the last five years, OTS has begun to take a more active role in encouraging certain fields of research.

In 1985, station usage averaged 22 persons/day. Seventy percent of this usage was by researchers, 20% by courses and natural history groups, and 10% by OTS staff and visitors. More than 100 separate research projects were carried out, and several dozen university, high-school, government, and natural history groups also used the station. In 1986 a new complex containing an expanded dining room, two dormitories, and a new workshop was completed; the new facilities will undoubtedly lead to even higher levels of usage.

History and Development of the Sarapiquí Region

La Selva is located at the junction between the flat Atlantic lowlands and the foothills sloping steeply up to the 2,900 m-high Barva Volcano. The

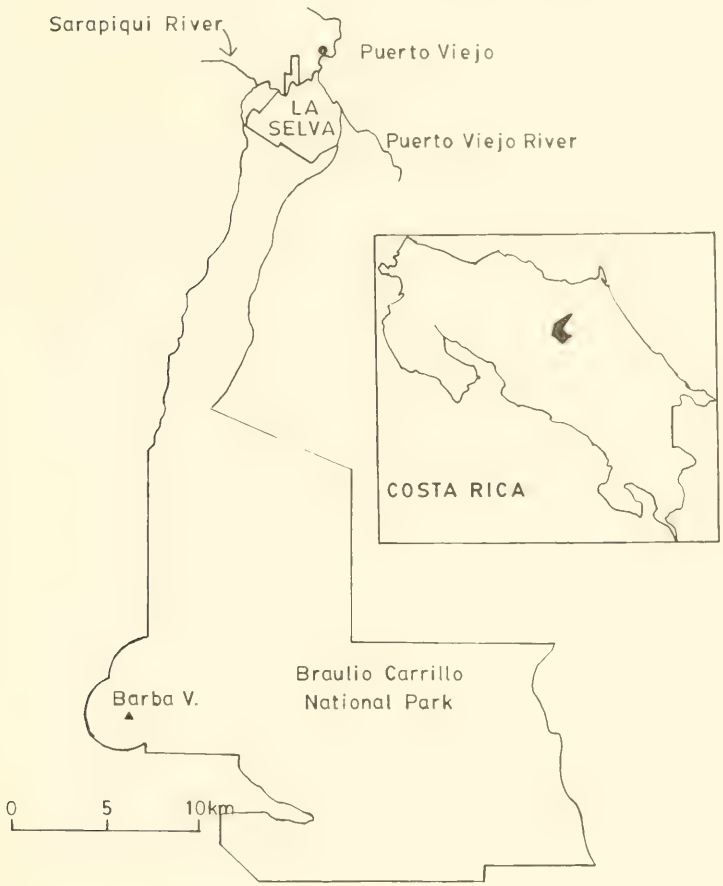

Fig. 1. The location of La Selva Biological Station in the Atlantic lowlands of Costa Rica.

region is called "Sarapiquí," after the principal river that drains the area. The dominant climatic factors are rain and heat. The mean annual temperature is 26° C, and rainfall averages 4 m annually. The natural vegetation of the area is tropical rainforest (tropical wet forest in the Holdridge life zone classification, Holdridge et al. 1971).

Transport in the region has always been difficult. In colonial times the rivers were the principal routes of commerce. Boats traveled from the Caribbean up the San Juan and Sarapiquí rivers to the head of navigation at Puerto Viejo ("Old Port,"), where mule trains departed on a miserable mud track for the long trek to the highland Central Valley. In the last two decades roads

have penetrated the region, and with them has come a vertiginous wave of deforestation.

Deforestation has different causes in different tropical countries. In the Sarapiquí region, the timber industry is not a primary cause of forest conversion. Most lumbering is simply extracting the marketable trees, and noncommercial species that don't get in the way of this exploitation are left standing. The result is a logged-over forest scarred by eroded extraction roads but still covered with trees.

Forest conversion in Sarapiquí, that is, removal of all tree cover from forested areas, is due almost entirely to clearing for agricultural use. This is not a new practice. Lands along rivers have been cleared for decades, in some cases probably repeatedly over centuries (Michael Snarskis, pers. comm.). These flat areas on reasonably fertile alluvial soils can, with proper management, support permanent agriculture, at least of some crops. What is new in the region, however, is the push of deforestation away from the flat alluvial plains up onto the steep foothills. The soils of these slopes are not alluvial and are notably acid and nutrient-poor. Conventional agriculture is not possible, and the predominant land use is low-quality pasture for cattle.

Clearing land for pasture devastated Costa Rica's forests. Between 1950 and 1973 the amount of pasture land increased 247% (Hartshorn et al. 1982). The driving force behind the chain saw is the developed world's appetite for beef; local beef consumption has actually dropped in recent years (Myers 1979). In Sarapiquí, large holdings of fertile alluvial land that could support agriculture are dedicated instead to cattle production. Cattle raising represents an affordable and socially acceptable way of obtaining a rapid economic return from a deforested area.

On the steep slopes, much of the clearing is done by colonists, who are supported by Costa Rica's agrarian reform laws. A colonist gains certain legal rights to land as soon as he removes the forest, and he can eventually acquire title to his homestead. A typical colonist will stake out 10-40 ha of forest by cutting boundary lanes. He proceeds to clear some section of this and plant pasture by broadcasting grass seed among the fallen trunks. In many cases the timber is not even removed due to the difficulty of access. On steep slopes these pastures are unproductive, highly susceptible to erosion (Fig. 2), and quickly invaded by woody scrub (Fig. 3). The farmer eventually either sells the land or abandons the pasture. Abandoned pastures quickly fill with luxuriant second-growth vegetation (locally called "charrales"); these areas represent an increasingly common vegetation type of the Sarapiquí region.

Why do people continue to colonize these areas? One answer is that there are many people without work or land. The population growth rate of Costa Rica is relatively high (around 2.6%, Hartshorn et al. 1982), and the growth

Fig. 2. Marginal land use in the Sarapiquí region of Costa Rica. Conversion of unsuitable slopes from forest to pasture and subsequent overgrazing lead to soil erosion. Photo courtesy of Catherine M. Pringle.

rate in the rural Sarapiquí area is probably higher. A recent OTS course survey in Puerto Viejo found the average family size to be eight! Also, there is substantial immigration from other parts of Costa Rica. The good alluvial lands have been taken, and what remains are the steep slopes with poor soil. Land colonization for speculation is also commonplace.

This type of development has left the region with many pressing problems. How can the rich biological diversity of the area be preserved? How can local ecosystems be managed to provide critical "environmental services" such as flood protection, soil conservation, and water supplies (Myers 1984)? What types of land use will be sustainable over the long term and at the same

time generate employment and earn foreign exchange? Part of the resolution of these issues depends on social and political solutions. However, there is a great deal yet to be learned about management of tropical ecosystems. In particular, stable and productive land uses that avoid the collapse of environmental services and mitigate species loss are urgently needed. I refer to these sustainable and ecologically rational land uses as "ecodevelopment" (Golley 1983). To develop these possibilities, research is required, professionals must be trained to carry out these studies, and the results of current investigations must be incorporated into the educational process. Research and education are the primary goals of OTS, and it is here that the biological field station can contribute to ecodevelopment of the surrounding region.

A Taxonomy of Research

At La Selva there are dozens of new research projects each year. The variety of subjects is impressive; while one researcher scrapes algae from a sloth's hair, another perches 30 m above the ground to watch migrating birds, and yet another connects sensitive vibration sensors to leaves to "listen" to a spider's delicate mating dance. One way of classifying these diverse projects

Fig. 3. Active pasture being invaded by woody brush. Many pastures on poor soils are eventually abandoned when the cost of clearing out weedy invaders becomes uneconomic.

is to assess whether the investigation directly addresses some immediate practical need ("applied research"), or instead is research carried out solely to answer a scientific question ("basic research"). This dichotomous classification is singularly unsatisfactory for describing the studies carried out at La Selva. Some projects do indeed fit neatly into one or the other box, but many do not. In a system such as a tropical rainforest, where so little is known about even the most basic properties of the biota and ecosystems, the distinction between basic and applied becomes vague. For the purposes of this article, I arbitrarily divide research into three categories: taxonomy, the discovery and description of species; studies at the sub-individual, individual, or population level (roughly physiology, behavior, and ecology); and research at the community or ecosystem level. With this simplified classification, I will discuss research in each area at La Selva, and describe how these investigations are or could be related to ecodevelopment of the region.

TAXONOMY: THE KEY TO THE STOREHOUSE

If tropical forests are a storehouse of biological diversity, then taxonomy is the science that can unlock the doors to these riches. The naming of species and placing them in some degree of relationship to the rest of the world's biota is a critical first step in biological research. While the immense richness of tropical rainforests is becoming better known, little is known about most tropical groups. For example, the trees are one of the best known groups at La Selva. For more than 30 years, a long line of distinguished tropical foresters has scrutinized these forests. In 1980, the list of La Selva trees stood at approximately 320 species. During the following five years, intensive collecting by the Flora of La Selva project increased that number to over 450 species (Gary Hartshorn, pers. comm.)! While tree diversity is of utmost interest to ecologists, the information gained by years of collecting and taxonomic research is not just of academic value. A sound understanding of the trees of Sarapiquí is necessary to manage natural ecosystems of the region. When the Costa Rican Forest Service (Direccion General Forestal, DGF) initiated large-scale natural forest management and inventory in the region, DGF scientists relied heavily on publications, collections, and expertise in dendrology developed at La Selva.

While the trees are a relatively well-known and manageable group, the insects of La Selva represent the taxonomic equivalent of a black hole. Even though insects are probably the most diverse group of animals in tropical forests and frequently interact strongly with human health and agriculture, only a fraction of the species have been described. The inability to identify species has meant that research in insect ecology must at times be postponed

until the taxonomy of the group of interest can be worked out. For example, University of Costa Rica (UCR) researchers investigating economically important tephridid fruitflies began by working on taxonomy; ecological work depended on being able to reliably recognize different species. A similar situation occurred with a UCR mosquito project. Although the primary aim of the research was to study the ecology of disease vectors, the team decided that the first step had to be unraveling the taxonomic mysteries of this group.

Taxonomic research is needed on a variety of groups important to ecodevelopment, including timber trees, medicinal and food plants, and insects of agricultural importance. La Selva is an active center for research in this area, since it offers a well-equipped base of operations as well as easy access to both undisturbed and altered habitats. The quest to identify the elements of biological diversity is not usually thought of as part of the economic development of a region. In the humid tropics, where in many groups the number of unnamed species exceeds the number of described ones, taxonomy has an important role to play.

UNDERSTANDING THE PIECES: PHYSIOLOGY AND WHOLE-ORGANISM BIOLOGY

The majority of research at La Selva up to now has been in the areas of physiology and ecology. Most of these projects were designed as basic research, but many are producing useful data and ideas applicable to development. One example at the physiological level is the Physiological Ecology of Tropical Trees project. The project group (Boyd Strain, Ned Fetcher, Steven Oberbauer, and Gilbert Rojas) has concentrated on growth, photosynthesis, and water relations of tropical trees, especially in the seedling stage. The results are basic for understanding tropical plant physiology, and in the case of commercial timber species, they are directly transferable to reforestation efforts.

Ecological research on individual species is also producing useful results. For most animals, basic information such as home range and average population density is not available. These data are needed to evaluate current efforts to protect biological diversity in the region and to design management programs. For example, how much area is required to protect a viable population of bushmasters (*Lachesis muta*), the largest pit viper in the world? Harry Greene (University of California, Berkeley) and Manuel Santana (UCR) are obtaining this information by inserting radio transmitters into snakes and following their movements and behavior for weeks at a time. The movements of very mobile animals such as large mammals and birds are more difficult to study. Bette Loiselle and John Blake (University of Wisconsin-Madison) and Gary Stiles (UCR) are investigating the altitudinal migration of

birds between the highland Braulio Carrillo Park and La Selva. The data on migration patterns and minimum habitat requirements will help the Costa Rican National Park service manage the new, expanded Braulio Carrillo Park (Stiles, this volume).

Research on basic ecological processes can produce surprising results. An investigator studying the reproductive biology of palms discovered a previously undescribed major pollinator of the widely cultivated peach palm, *Bactris gasipaes* (Beach 1984). George Schatz, who worked on pollination of rainforest Annonaceae for his Ph.D. dissertation, found his expertise in demand when local guanabana (*Annona muricata*) plantations showed low levels of fruit set.

Forestry-related research at La Selva is particularly active and important. Much of this region has potential for forestry, but little reforestation and almost no forest management is currently practiced. This is particularly unfortunate as Costa Rica will shortly become a net importer of wood products (Hartshorn et al. 1982). A long-term forest inventory project has followed tree growth and mortality on 12.4 ha of primary forest for 15 years (Lieberman et al. 1985). Its results indicate that the La Selva forest is exceedingly stable at the ecosystem level but highly dynamic at the level of an individual tree. The total number of trees in the plots varied less than 2% over 13 years, but 23% of the individuals died. This study is fundamentally important for understanding the productivity and functioning of the region's natural vegetation. Deborah Clark and I are studying the regeneration of commercial timber species in primary forest; the results will show which species merit further study for use in sustained-yield systems. Although the project was begun as basic research, our findings on light environments of saplings (Clark and Clark 1987) indicate lines of research that should be pursued to maximize production in managed forests. Once promising timber species are identified, research is required before they can be commercially utilized. Seeds must be collected; this requires data on fruiting seasonality. Germination requirements must be determined and growth trials must be carried out. Projects in all these areas are underway at La Selva (Fig. 4). The Costa Rican Forest Service and OTS are collaborating on growth trials of promising native tree species. Because these experimental plots are located at an active research station, they will also serve as foci for additional studies in herbivory, physiology, and genetic diversity; these results should further enhance the knowledge available to be channeled into economic development.

UNDERSTANDING THE WHOLE: COMMUNITY/ECOSYSTEM RESEARCH

Ecosystem research at La Selva has concentrated on two main areas:

the role of tree-fall gaps in primary forest structure and function, and the measurement of water and nutrient flows and processes in primary and disturbed habitats. Hartshorn's seminal studies of La Selva's forests (Hartshorn 1978, 1980) stimulated a series of investigators to examine plant and animal distributions and ecological processes in relation to natural tree-fall gaps. The most ambitious effort to date is a multi-disciplinary project comparing light environments, plant colonization, herbivory, and nutrient processes in gaps and forest understory (Julie Denslow, Jack Schultz, Peter Vitousek, Boyd Strain, and Ana Gomez). Such information is crucial to understand how primary rainforest functions, and also to serve as a benchmark against which managed systems can be compared.

Two well-known characteristics of tropical rainforest are abundant water and, in many areas, infertile soils. Both water and soil biology are areas of active research at La Selva. How does water flow through these soils? What nutrients are limiting plant growth? How do nutrients move through these systems? What processes function in primary forest to maintain long-term stability and productivity? How do these processes compare to managed systems, which tend to be highly unstable and productive only in the short run? The answers to these questions are critical for designing sustainable managed systems.

Because little is known about ecosystem processes in the humid tropics, basic research in this area is urgently required. One multi-investigator team is attempting to describe water and nutrient processes in early second-growth forests on abandoned pastures. Both descriptive and experimental approaches are already yielding surprising insights. The simple act of workers removing the grass on an experimental plot produced significant soil compaction (Radulovich and Sollins 1985). Simple models of water filtration do not apply in these soils because much of the water drains through large macropores (Ricardo Radulovich, pers. comm.). Other investigators have analyzed the flow of water and nutrients on the infertile hillside forests that are now being cleared for agriculture (Luvall 1984; Parker 1985). Stream biologists are comparing nutrient flows and plant and animal communities in streams from primary forests and from disturbed areas. The initial results suggest that nitrogen and phosphorus may not be limiting in local streams from pristine watersheds (Pringle et al. 1986). Preliminary data on fish communities suggest that these pristine watersheds may be important breeding grounds for fishes that as adults live in rivers in developed areas (Janet Burcham, pers. comm.).

Tropical ecosystems are inherently more complicated than temperate ecosystems. The same biological diversity that makes these forests so interesting and valuable also insures a daunting complexity in community processes. Ecosystem investigators at La Selva are just beginning to understand some of the higher-level properties of these habitats.

EDUCATION AND ECODEVELOPMENT

OTS was founded by educational institutions that saw a need to teach tropical biology. For years La Selva has been the most active of OTS's training centers for graduate students. While this is still true, in the last few years OTS has taken a broader view of its role in education and has developed several new teaching initiatives. At all levels these activities affect ecodevelopment.

The greatest impact OTS has had on tropical biology has been through teaching tropical biology to graduate students. During its 25 years of existence, more than 1500 students have taken OTS courses. This steady stream of enthusiasm and talent has made Costa Rica one of the tropical countries most studied by North Americans (Clark 1985). Besides North Americans, many Latin American students have received advanced training through OTS courses. The population ecology course taught in Spanish draws students from all over the Neotropics. Ecodevelopment needs have been addressed in courses in tropical forestry, geography, parasitology, meteorology, and agricultural ecology. Through these courses a broad base of scientists has been trained to work on tropical problems. Many of the research projects described above have been carried out by investigators who first became interested in tropical problems via an OTS course. The effects are evident throughout the governments of the United States and many Latin American countries where a surprising number of OTS graduates are involved in national research and development and environmental management agencies. The initial exposure and training of several generations of tropical scientists has been one of OTS's finest achievements.

Undergraduate courses from Costa Rican universities also regularly use La Selva. The students get a first-hand look at research in an active field station, and some of them later return to work as researchers or technicians at the station. Undergraduate and extension courses from the U.S. find the station an excellent site for an introduction to humid tropical forest. As with the OTS courses, alumni of these visits form a group of highly educated and potentially influential professionals sympathetic to the problems of tropical countries.

A totally different type of use is what is called "ecotourism" in Costa Rica. Groups of non-scientific visitors interested in natural history are allowed at the station on a space-available basis. Visitors receive talks from OTS staff on tropical deforestation and Costa Rica's national parks, as well as information on current conservation campaigns.

During the 1960s and 70s there was comparatively little research activity at La Selva. The station consisted of a few small buildings surrounded by forest and accessible only by boat and was used mainly by North Americans.

This has changed in recent years. Usage has doubled in the last 5 years, and the physical plant has greatly expanded to service this increase. Costa Ricans now account for over 30% of current station usage. Deforestation has arrived at La Selva's doorstep, although the station and the neighboring protected forests to the south are still intact. These factors have combined to change La Selva's relations to the local community, of which Puerto Viejo is the seat of government. OTS's former policy of benign neglect of community relations has been replaced by an active policy of response to local concerns, and the development of a flourishing environmental education program. Students and teachers regularly visit the station for organized tours and lectures from researchers. In the future, OTS hopes to ensure that a normal part of going to school in Sarapiquí includes visiting La Selva and discovering first-hand what biological research is about. The students of today will be the community of tomorrow. For the long-term security of La Selva, it is important that residents of the region recognize the value of this world-class research center and come to appreciate the importance of biological research to regional development.

STRENGTH THROUGH DIVERSITY: THE LA SELVA SYNERGISM

It is clear from the above descriptions of research, teaching, and environmental education that a broad range of activities take place at La Selva. I believe one of the most valuable assets of the station is this diversity. Most research stations developed as outgrowths of single departments or institutions. As a rule, agriculture or forestry stations are physically separate from zoology/botany stations. Because La Selva is operated by a consortium of universities, it has not developed along traditional departmental lines. Research has tended to follow the facilities available. Physiological and ecosystem research expanded rapidly following the arrival of 24-hour electricity and construction of a modern laboratory building. Forestry trials and research on altered habitats began in earnest when large areas of secondary habitats were added to the original reserve.

The outcome of this type of development has been a unique mixing of researchers of different disciplines from widely differing institutional settings. Life at an isolated research station encourages this mixing. All scientists, students, and visitors share a common dining room. This prosaic necessity, I think, is a benefit, since it helps ensure communication among all station users. Another synergistic force is the program of seminars given by researchers. Academic scientists are well aware of how even small distances between buildings can isolate different research groups. This barrier is non-existent at La Selva, and the mix of scientists attending any seminar is quite heterogeneous.

The interaction between students, visitors, and scientists is also interesting. All scientists at La Selva are working on their own research, and are under time and money constraints to do the greatest amount of field work in the shortest time. Nevertheless, every academic course that visits La Selva succeeds in recruiting "volunteer" researchers to give lectures, lead orientation walks, or guide field problems. Researchers also participate in the environmental education program directed at local residents.

Non-scientist visitors interested in natural history also share living and eating facilities with the researchers and students. La Selva, as an active research station located adjacent to one of the world's great rainforest national parks, offers a rare opportunity for visitors to enjoy and learn about tropical rainforest in relative comfort. For many it is also a first chance to observe field research. As a rule these visitors are interested in natural history and the tropics and frequently are willing to contribute time and money to conservation efforts. OTS has up to now encouraged natural history groups to use La Selva in off periods. It remains to be seen how this type of use will fit in as the station grows and overall usage increases. I think it is worth considerable effort to find ways to continue this type of usage of La Selva. In the long run, these visitors will form a corps of interested supporters of tropical conservation and research. Given the seriousness of tropical deforestation, this is an opportunity that should not be missed.

THE FUTURE

In 1980 the National Research Council of the United States commissioned a study to recommend strategies for maximizing progress in tropical biology. The report, prepared by an international committee of scientists, emphasized the value of building up intensive databases in a few sites. They recommended that tropical ecosystem studies be concentrated at four different stations; La Selva was one of those selected (National Research Council 1980). The committee specifically recognized the research value of the great altitudinal transect of forest that stretches from the station to the peak of Barva Volcano. Events to date at La Selva and prospects for the future indicate that the committee's suggestions were well founded.

A noteworthy attraction of La Selva is the wealth of knowledge now available about its ecosystems and biota. It is true that only the surface has been scratched, but compared to most tropical forests, La Selva is well studied. As the NAS committee foresaw, many future projects will be begun at La Selva primarily because an initial database has been built up there. Increased research will fund improved laboratory facilities, and that in turn will make possible increasingly sophisticated types of research.

Applied research will increase rapidly in the next few years. Agencies such as World Bank and U.S. A.I.D. are increasingly aware of the environmental impacts of development projects (Baum and Tolbert 1985) and are now funding research on how to avoid environmental problems. Many academic researchers are very willing to undertake applied problems in their field, if they can find ways to collaborate with projects in developing countries. La Selva, by attracting a broad range of scientists from numerous disciplines, will increasingly serve as a catalyst to link academic biologists to development-related problems.

It is safe to predict that overall research usage at La Selva will climb sharply. The infrastructure of the station is in itself a magnet to researchers who need laboratory space next to rainforest habitats. The availability of disturbed habitats that can be experimentally manipulated is already attracting many kinds of studies. The extension of Braulio Carrillo National Park (see Pringle, this volume) opens new opportunities for basic ecological and taxonomic research. There are unfortunately very few sites in the Neotropics where scientists can carry out field research in tropical rainforest with relative ease. Costa Rica, a democratic and stable country, has historically been a generous host to foreign scientists (Clark 1985). The combination of positive host-country relations, protected research sites in primary and altered habitats, and adequate laboratory and logistic support will serve to increase overall research at La Selva.

Every research station is unique in its social, biological, and scientific setting. The La Selva Biological Station, with its diversity of habitats, researchers, and visitors, is one example of how international cooperation can lead both to the conservation of biological diversity and to the search for solutions for pressing development problems.

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HISTORY OF CONSERVATION EFFORTS AND INITIAL EXPLORATION OF THE LOWER EXTENSION OF PARQUE NACIONAL BRAULIO CARRILLO, COSTA RICA

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The Braulio Carrillo Park extension (Heredia Province, Costa Rica) is a 22-km long land corridor that stretches in a southwesterly direction from the southern boundary of La Selva Biological Station (of the Organization for Tropical Studies) to Parque Nacional Braulio Carrillo, a 31,400-ha park in the mountains of Costa Rica's Cordillera Central. The La Selva-Carrillo transect encompasses a topographic gradient of diverse primary rainforests unmatched in all of Central America. It spans elevations from about sea level to almost 3,000-m elevation in a distance of only 35 km. On 13 April 1986, President Luis Alberto Monge of Costa Rica officially incorporated the 13,500 ha encompassed by the land corridor into Parque Nacional Braulio Carrillo.

This paper documents the history of the effort to protect the park extension and adjacent lands in the hope of encouraging similar international efforts toward the conservation and sustained use of natural resources in the tropics. The endeavor was characterized by an unprecedented collaboration that involved the Costa Rican National Parks Foundation and National Park Service, international conservation organizations (Nature Conservancy, World Wildlife Fund-US), the scientific community (e.g. Organization for Tropical Studies-OTS), numerous philanthropic groups (e.g. MacArthur Foundation), and the private sector. Though international or foreign conservation groups have played critical roles in helping Costa Rica establish and consolidate parks and other protected areas, this conservation effort is unique in that virtually all of the funds for land acquisition were raised outside of Costa Rica.

This contribution also highlights biological results of the first OTS-sponsored expedition into the park extension in January 1983, which was conducted with the objectives of aiding land

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protection efforts and stimulating additional research in the area. The observations of nine scientists during a ten-day foray into the land corridor form the basis of an ecological commentary on land use, hydrology, flora, and fauna.

An Organization for Tropical Studies field biology course in Costa Rica during 1982 marked my introduction to the splendor and biological complexity of tropical rainforests. The course provided invaluable exposure to basic natural history and ecological theory. It also increased my awareness of the many problems confronting developing countries in their efforts to protect their biological heritage. At that time, the imperiled existence of tropical systems was underscored by an immediate crisis in OTS's backyard: increasing deforestation of land surrounding La Selva Biological Station threatened its continued use as an effective center for field research and ecodevelopment.

OTS courses are conducted at a fast pace and at a variety of field sites to expose students to a wide range of different habitats during the short eight-week time frame available. As we traveled around the country, we developed a disquieting awareness of the patchy and isolated occurrence of the habitats that we were studying. As our OTS bus lumbered up into the Cordillera de Tilarán, the deforested and eroded slopes of Guanacaste unfolded below us; when we disembarked in a pasture on the banks of the Río Puerto Viejo, after a two-hour drive through pastureland dotted with grazing Brahman cattle, it was startling to learn that the remote La Selva Biological Station was just across the river. And later, while we were busy counting castes of leaf cutter ants near La Selva's Central Trail, our class was passed by a group of Costa Ricans, visiting from the nearby town of Puerto Viejo. They were marveling at the forests that once covered their own lands and talking excitedly at their first glimpse of a monkey in the wild.

It is through experiences such as these that an OTS student perceives the deterioration of tropical systems in the context of the changing fabric of the country. Even in Costa Rica, with its unparalleled conservation record and widely acclaimed park system, at the present rate of rainforest destruction the exposure of future generations to the lore and natural history of the forest may soon be limited to their grandfather's reminiscences of hunting tepezcuintle (a cat-sized rodent) and holiday picnics at Parque Nacional Volcán Poas.

What can be done to offset the rapid destruction of tropical forests? How can the scientific community exert an influence? Unfortunately, conservation issues as well as some aspects of applied biology have often been labeled as intrusions into the "objective" realm of science. In turn, many scientists

conducting basic research have been criticized for adopting an ivory tower or elitist approach. Such attitudes influence the direction of scientific research, often precluding interdisciplinary approaches to complex problems and sending conflicting signals to the developing countries where we work. The overriding reality of rapid, global rainforest destruction underscores the bottom line: if the present trend continues, the objects of scientific inquiry will disappear forever and developing tropical nations will find themselves stripped of irreplaceable natural resources. The Organization for Tropical Studies provides students of biology with the scientific training and opportunity to promote sustainable development and conservation of tropical resources.

A HISTORY OF THE EFFORT TO PROTECT THE BRAULIO CARRILLO PARK EXTENSION

The 13,500-ha park extension (Fig. 1) stretches in a southwesterly direction from La Selva Biological Station (1,336 ha) at 36 m, to the northern border of the 31,401-ha Parque Nacional Braulio Carrillo, which extends up to 2,906 m elevation at the summit of Volcán Barva (Fig. 2). The entire 2,870-m La Selva-Braulio Carrillo transect stretches over a linear distance of 35 km. The park extension (Fig. 1) includes: (1) a 3-6 km wide and 18 km long portion between the Río Peje and Río Guácimo on La Selva's southern boundary (La Zona Protectora La Selva); (2) a former forest reserve (Reserva Forestal); and (3) additional private lands west of Braulio Carrillo Park and the Forest Reserve.

The history of the park extension conservation effort merits recounting because it transcends traditional boundaries between disciplines. It represents a success story resulting from a combination of happenstance and dedication on the part of many people from different nations, organizations, and perspectives. This collaborative effort is also the force that brought this rainforest symposium to fruition. Its development is briefly documented here with the hope of encouraging similar cooperative and international efforts toward the conservation and sustained use of natural resources in the tropics.

Throughout the years, OTS's La Selva Biological Station has become increasingly isolated by deforestation on its northern, western, and eastern boundaries. Were it not for the following developments, the station would surely have become an island of forest in a sea of cow pasture.

During the summer of 1977, Thomas S. Ray Jr. became concerned about the increasing ecological isolation of La Selva while working at the research station as a graduate student from Harvard University. He decided to try to organize support for the purpose of expanding La Selva boundaries southward to include the complete watersheds of major streams draining the

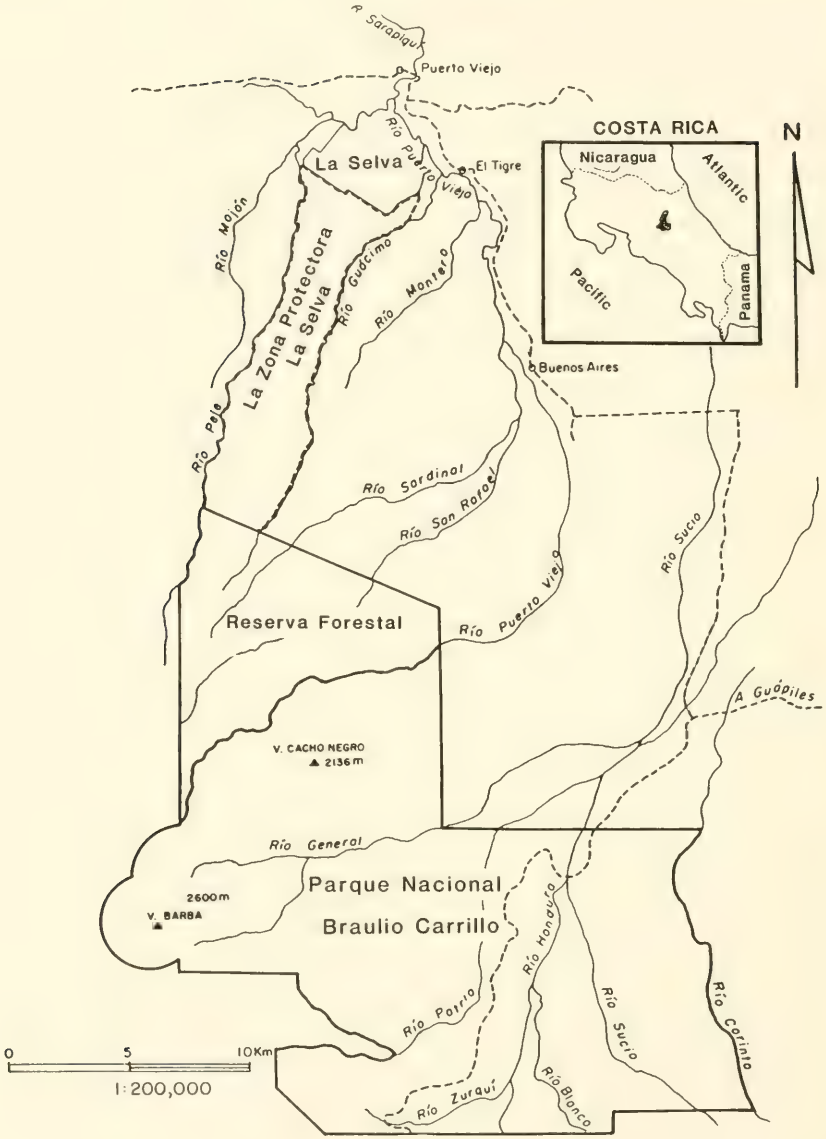

Fig. 1. Location of Parque Nacional Braulio Carrillo, Reserva Forestal, La Zona Protectora La Selva and La Selva Biological Station in Costa Rica. Figure modified from Hartshorn and Peralta (this volume).

property (D. Stone, T. Ray, pers. comm.). Among many others, Ray brought the issue to the attention of Thomas E. Lovejoy, then program director of the World Wildlife Fund-US. After the two examined maps of the area, they began thinking on a much larger scale, considering the possibility of creating a national park contiguous with La Selva. Ray identified a large government forest reserve 15 km to the south of La Selva and proposed the idea of establishing a corridor between the two areas. In the meantime, unknown to them, a national park was being planned within this forest reserve by the Costa Rican government. On 24 August 1977, Braulio Carrillo National Park was established by presidential decree for the purpose of providing watershed protection for a road project that would connect San Jose with Guápiles, a town in the Caribbean lowlands southeast of La Selva (Boza and Mendoza 1981).

In late 1977, Lovejoy met with President Daniel Oduber of Costa Rica, concerning protection of the land corridor as an extension of Parque Nacional Braulio Carrillo. Though President Oduber expressed interest in this idea, he left office soon after without taking action. Meanwhile, OTS was busy on another front, struggling to raise funds for purchase of a 631-ha tract on its western boundary (the "Vargas Property"). The Costa Rican Park Service also had many other pressing commitments and was struggling to protect existing parks, with severely limited funds.

Throughout the next four years, many concerned individuals from scientific institutions and conservation organizations pushed for protection of a land corridor between Braulio Carrillo and La Selva. In April 1982, Luis Diego Gómez of the Museo Nacional de Costa Rica urged President Rodrigo Carazo of Costa Rica to protect the proposed land corridor from further development.

On 28 April 1982, shortly before his term ended, President Carazo issued a decree that officially designated the lower portion of the much-sought-after land corridor (7,368 ha including La Selva) as "Zona Protectora La Selva." Protection zone status means that land owners can continue existing farming practices, but conversion or alteration of forest is prohibited. This measure was viewed as a temporary holding action while funds were sought to incorporate the lands into a national park. Since government funds that might have been used to buy out private holdings had been depleted by one of the most severe economic crises in the country's history, it became clear that a large portion of the money for land purchase had to be raised outside of Costa Rica. The OTS Board of Directors immediately voted to donate $30,000 to the Costa Rican National Parks Foundation to support the necessary park service personnel for enforcement and also to encourage initial fund-raising activities by the Foundation.

In November 1982, after completing an OTS course and learning about

Fig. 2. Aerial photograph of Parque Braulio Carrillo terrain (Volcán Barva, center peak) sloping down into Zona Protectora La Selva. Photo courtesy of Robert L. Sanford (1978).

the Zona effort, I proposed an expedition into La Zona Protectora to collect biological information that could be used in the continuing effort to protect the corridor. Donald E. Stone, executive director of OTS, funded the proposal from a block fellowship grant provided to OTS by the Jessie Smith Noyes Foundation. In January 1983, a group of nine biologists from the United States and Costa Rica explored the Zona for ten days, making observations that confirmed the biological richness and importance of the area.

Serendipity entered the scene here. On a bird-watching excursion in Costa Rica in 1984, Murray Gell-Mann, a Nobel laureate in physics from the California Institute of Technology, heard about the Zona effort from tour guide Bret Whitney. By good fortune, Gell-Mann was a member of the Board of Directors of the John D. and Catherine T. MacArthur Foundation in Chicago and chairman of its Committee on World Environment and Resources. He was so impressed with the ecological importance of the Zona that he approached the World Wildlife Fund and the Nature Conservancy at the Global Possible Conference (sponsored by the World Resources Institute) later that year to ask about the status of the effort to preserve the area. He learned that the estimated purchase price of the land was two million dollars, and that no

major fund-raising effort was yet underway. As a result of Gell-Mann's inquiries, the International Program of the Nature Conservancy presented a proposal to the MacArthur Foundation. With guidance from many leading biologists and conservationists, the board voted unanimously to grant one million dollars, on a one-to-one challenge basis, towards the purchase of the land for incorporation into the Costa Rican Park System. The grant was given to the Nature Conservancy on 14 December 1984, and shortly thereafter, a consortium was formed, including the Nature Conservancy, the World Wildlife Fund-US, the Organization for Tropical Studies, the Costa Rican Park Service and the Costa Rican National Parks Foundation, all dedicated to raising the balance of funds by 31 December 1985.

Kenneth R. Margolis, formerly director of development of the Nature Conservancy's International Program, orchestrated this cooperative effort and, as he informed us at the rainforest symposium on 28 September 1985, the fund-raising effort at that time was three-fourths of the way towards its goal. Private donations resulting from the symposium came to approximately $30,000 and, by the 31 December deadline, over $1,095,000 had been raised to match the MacArthur challenge grant. Funds in excess of those needed for land acquisition in the Zona were used to purchase private inholdings in the forest reserve and adjacent areas.

Less than ten years after the idea of protecting a land corridor between La Selva and Parque Braulio Carrillo was conceived, it has become a reality. On 13 April 1986, President Luis Alberto Monge officially incorporated 13,500 ha, encompassed by the upper Zona land corridor (excluding La Selva Biological Station)[1] and adjacent forest reserve, into the Costa Rican National Park System as an extension of Braulio Carrillo Park (Fig. 3)!

Meanwhile, additional evidence for the tremendous biological diversity encompassed by the La Selva-Braulio Carrillo land transect is accumulating. In 1985, an Operation Raleigh venture (U.K. organized) was conducted over a three-month period under the direction of John Proctor (Chief Scientist in the Field) of the University of Stirling. Interconnecting trails and campsites were implemented to facilitate establishment of a series of forested 1-ha plots every 500 meters for long-term ecological research (see Hartshorn and Peralta, this volume). In April, 1986 an OTS scientific team funded by the National Geographic Society mounted a major biological expedition into the transect. A team of some 30 scientists is presently compiling and analyzing data and information from this expedition. An effort is also under way to have the entire La Selva-Braulio Carrillo transect and adjacent non-park lands designated as an international biosphere reserve through UNESCO's Man and the

[1] The northern boundary of the Braulio Carrillo park extension is marked by the southern boundary of La Selva Biological Station.

Fig. 3. President Luis Alberto Monge signing decree that officially incorporated La Zona Protectora La Selva into Parque Nacional Braulio Carrillo (La Selva Biological Station, April 13, 1986). Photo courtesy of Gregory G. Dimijian.

Biosphere Programme. Fund-raising efforts are now focusing on the development of a long-term management plan and endowment for the entire Parque Nacional Braulio Carrillo.

ECOLOGICAL AND SOCIO-ECONOMIC CONTEXT

The incorporation of the La Selva-Braulio Carrillo transect into the Costa Rican Park System represents a significant conservation breakthrough on both a regional and continental level because no similar transect of primary forest spanning these elevations is protected elsewhere in Costa Rica or all of Central America. In Costa Rica, protected wildlands in highland areas, such as La Amistad Park and the Hitoy-Cerere Biological Reserve, are isolated from undisturbed lowlands. Similarly, parks in the lowlands, such as Tortuguero and Corcovado National Parks, are entirely isolated from upland areas. A salient feature of the La Selva-Braulio Carrillo transect is that the change in elevation is relatively gradual, resulting in fairly large middle elevation areas. As the following expedition account and subsequent papers attest, these

areas and their corresponding biota are little known relative to other elevations and are underrepresented within existing parks and protected areas in Central America (Grayum, pers. comm.; Hartshorn 1983). Furthermore, the location of this elevational transect next to La Selva Biological Station has tremendous significance for science and ecodevelopment in tropical countries (see Clark, this volume). Though it remains to be seen if the narrow corridor can serve as a viable protected area in perpetuity, the acquisition of the area represents an important step in conservation.

Created just 17 years ago, Costa Rica's national park system now protects half a million ha (over a million acres) in approximately 22 parks and reserves. This park system is internationally acclaimed, representing a stellar achievement among developing and developed countries alike. Though international or foreign conservation groups have played critical roles in helping Costa Rica establish and consolidate conservation units, the Zona conservation effort is unique in that virtually all of the funds for land acquisition were raised outside Costa Rica. This has not been the case in past park consolidation efforts and the Costa Rican Park Service has become financially overextended, with its problems compounded by the serious economic crisis affecting the nation. For instance, of the 2.2 million dollars necessary to establish Corcovado National Park in 1975, only $265,000 came from outside sources. The toll extracted by Corcovado on the Costa Rican people, economy, and park system is still being felt with the recent and costly eviction of the many gold miners illegally residing in the area (Janzen et al. 1985; Tangley 1986).

The Zona conservation initiative indicates a new level of commitment on the part of a diverse group of organizations in developed countries. It represents an unprecedented collaboration between the scientific community, conservation organizations, philanthropic groups, the private sector, and the Costa Rican government and Park Service. The effort has transcended both real and perceived boundaries that have separated these organizations and paved the way for future collaborations. Economics alone indicate that conservationists, scientists, resource managers, and government officials alike would do well to analyze the events and forces that formulated the Zona campaign so that they can be extended to other situations and expanded upon. This paper documents the successful first phase of the Zona conservation effort. As pointed out by Luis Diego Gómez (this volume), "land acquisition means nothing without the proper management and institutional support that will guarantee perpetuation of the effort."

INITIAL OTS EXPEDITION INTO LA ZONA PROTECTORA LA SELVA

The funding of the 1983 expedition into La Zona Protectora La Selva

reflects OTS's active role in providing graduate students with opportunities to become involved in collaborative and interdisciplinary research ventures beyond the immediate funding priorities of many larger granting institutions. In my case, OTS has supported projects on a variety of different levels, from investigations of nutrient cycling in La Selva streams to the organization of this expedition. The 1983 Zona expedition was conducted with the objectives of stimulating additional research in the land transect and of collecting biological information to encourage the effort to convert the Zona into an extension of Parque Braulio Carrillo.

On 12 January 1983, nine US and Costa Rican biologists found themselves jolting along in a caravan of two Land Rovers and a tractor, negotiating the 17 km of muddy ruts from La Virgen de Sarapiquí to the Zona. Ironically, the local sawmill in La Virgen provided us with the tractor that carted our gear and supplies. Before the Zona was declared a protection zone, the tractor often made this trip without cargo, returning to the sawmill with heavy loads of timber harvested from the Zona and adjacent areas.

We established a base camp under the roof of an abandoned sawmill near the Quebrada Cantarrana at about 350 m elevation. The Servicio de Parques Nacionales de Costa Rica provided us with two excellent guides, Eladio López and Miguel Antonio Mena Rojas. With their assistance a network of trails was cut to make upper areas of the Zona accessible. We radiated out from our base camp, making natural history observations and collections that form the basis of the following ecological commentary on land use, hydrology, flora, and fauna.

Land Use

An estimated 73% of the Zona is in primary forest and the rest is in various states of disturbance, based on aerial photos taken in January 1983. At least 16% of the land area has been converted to pasture, with many of the trees left to rot where they were felled (Fig. 4). The remaining 10% is primarily secondary forest and less than 1% of the Zona is estimated to be in agricultural use. At the time of the expedition, all of the Zona was either legally titled as private land or was contested and claimed by squatters. At the time of publication of this volume, however, virtually all of the land holdings within the Zona and adjacent forest reserve have been evaluated, purchased, and incorporated into the Costa Rican National Park System.

Hydrology

The Zona is drained by two well-developed stream valley systems, the Río Peje and the Río Guácimo. These rivers are rare examples of relatively

Fig. 4. Inhabited finca in Zona Protectora La Selva (250 m). Photo by Catherine M. Pringle (January 1983).

undisturbed, high-gradient, tropical systems, dropping from 1600 m to near sea level in a distance of less than 25 km. Most of the Peje and Guácimo watersheds lie within the Zona and adjacent forest reserve.

The insured protection of the vegetative cover of these drainages is hydrologically crucial for groundwater stabilization in coastal plain areas such as Puerto Viejo and La Selva. La Selva receives about 4000 mm (157 inches) of rain per year; up to 150 mm (6 inches) of rain have fallen in just one day during the rainy season. High discharge in streams draining the Zona and Parque Braulio Carrillo can raise stream water levels as much as 9 m above normal levels at La Selva. The combination of heavy rainfall, steep topography, and shallow soil profiles suggest a disastrous scenario should the vegetation of contiguous highland drainages be significantly disturbed. In similar areas where rainforest has been converted to pasture, an estimated 400-800 tons of soil/ha/yr are eroded (Hartshorn et al. 1982). The topsoil is permanently lost to the ecosystem, clogging lowland rivers and often ruining drinking water supplies, not to mention fisheries and other resources.

Virtually nothing is known about the biology of rivers that drain undisturbed rainforest areas in Central America. Preliminary nutrient bioassays conducted in a stream that drains largely primary forest in the central portion of La Selva and the northern part of the Zona indicate that neither of the major nutrients (nitrogen or phosphorus) limited periphytic algal growth during a short period in the rainy season (Pringle et al. 1986). We found phosphorus levels in many streams draining La Selva and the Zona to be unusually high relative to other undisturbed streams in temperate areas. Watersheds in the Zona are underlain by volcanic basalt (as are many in Central America) and are generally characterized by young soils that contain more phosphorus relative to older soils typical of tropical areas such as the Amazon (Vitousek 1984). Virtually nothing is known regarding how this regional geochemistry is reflected by stream nutrient chemistry and primary production. The La Selva-Braulio Carrillo transect provides an unparalleled study site in Central America for aquatic biologists to study undisturbed, high-gradient streams. Hydrological studies alone would be of great significance to Costa Rica and other developing countries.

Ecological Life Zones and Woody Plants

The entire La Selva-Braulio Carrillo transect encompasses four life zones and two transition zones based on the altitudinal distribution of tree species (Holdridge et al. 1971). Holdridge life zones are bioclimatically defined units based on temperature, rainfall, and the seasonal variation and distribution of these two climatic factors as primary determinants of vegetation.

In the cooler and damper higher elevations of Parque Braulio Carrillo, a

cloud forest environment prevails, where tree ferns and epiphytes are abundant. These life zones (Tropical Lower Montane Rainforest and Tropical Montane Rainforest) are markedly different from the lower altitude forests of La Selva, which are classified into different zones (Tropical Wet Forest and Tropical Wet Forest–Cool Transition). La Selva Biological Station experiences a warmer climate, and forests are dominated by the legume, *Pentaclethra macroloba* (Mimosaceae). A striking aspect of La Selva forests is the richness and abundance of subcanopy and understory palms, of which there are nearly 30 species. This brief comparison of life zones on either extreme of the continuum highlights the diverse topographic gradient of primary forests encompassed along the entire transect.

Gary S. Hartshorn (Tropical Science Center, Costa Rica) examined altitudinal shifts in life zones on the expedition. He determined that two ecological life zones and two transitional areas occur within the Zona itself. Hartshorn oversaw the identification of ≅200 tree species and estimated that this probably constitutes less than one-third of the number of tree species to be expected in the entire Zona. He also found that the forests of the Zona were critical habitat for at least 75 tree species. The Zona is one of the few areas where these tree species can be preserved given the widespread destruction of similar vegetation types elsewhere. Although no information was available on the tree flora of Braulio Carrillo Park at the time of this initial expedition, it was projected that the entire La Selva–Braulio Carrillo transect could harbor as many as 800 tree species, or 40% of the number of trees in the entire country. A more detailed description of primary forests of the La Selva–Barva Volcano land transect is provided by Hartshorn and Peralta (this volume).

Herbaceous and Understory Plants

Michael H. Grayum (Missouri Botanical Garden), George E. Schatz (University of Wisconsin) and Isidro Chacón (Museo Nacional de Costa Rica) collected and oversaw the identification of primarily herbaceous and understory plants. Despite the limited time and specialized interests of these three botanists (which biased collections towards pteridophytes and the angiosperm families Araceae, Palmae, Cyclanthaceae, Piperaceae and Annonaceae), over 20 new herbaceous plant species were discovered (e.g. *Anthurium* sp., two *Monstera* spp. and *Euphorbia* sp.). Additionally, 12 plant species previously not known from Costa Rica were recorded. For instance, *Geonoma epetiolata*, a distinctive palm recently described from two collections in Panama (Moore 1980), was observed to be common in the Zona above 200 m. Some plant groups were found to be species-rich at lower elevations (e.g. Melastomataceae, Rubiaceae, and *Piper*), while others were more diverse at higher elevations (e.g. Sapotaceae, *Peperomia*).

Several species of economic importance, or closely related to economic species, were found to grow wild in the Zona, including the vanilla orchid, several genera of palms (e.g. *Euterpe*) valued for their heart of palm, and two species of *Theobroma* (cacao), the genus from which chocolate is derived. *Monstera deliciosa*, the wild relative of ceriman (an edible multiple fruit), was found growing sparsely in the Zona between 400-600 m. This species has been described as "rare in the wild" (Madison 1977), and preservation of wild genetic types could be significant to future breeding programs.

These botanical observations, made in just ten days by three botanists, point to the unrealized economic value of this poorly known flora, not only as a source of food, but of pharmaceutical products and all of the other applications that accrue from such tremendous genetic diversity.

Avifauna

F. Gary Stiles (Universidad de Costa Rica) and his assistant, Carlos Gómez (Universidad de Costa Rica), provided the ornithological expertise on the expedition. As Stiles provides a detailed discussion of avifaunal migrations in the Zona and adjacent areas (Stiles, this volume), I will confine my comments to more general findings.

During the short duration of the expedition, Stiles observed about 230 species of birds, estimating that ~400 species occur in the Zona. He estimates that the La Selva-Braulio Carrillo transect harbors 75-80% of the landbird species in Costa Rica, or as many bird species as found on the entire North American continent (Stiles 1983). River gorges within the Zona were found to be relatively unaffected by deforestation and serve as effective corridors for the movement of a variety of forest birds (e.g. fasciated tiger heron [*Tigrisoma fasciatum*], white hawk [*Leucopternis princeps*]).

Perhaps most importantly, Stiles determined that about 35 bird species utilize the land corridor for seasonal altitudinal migrations. Since these altitudinal migrants may spend several months in lowland forests, deforestation of the Zona would seriously threaten their survival. The emerald toucanet (*Aulacorhynchus prasinus*) is one such migrant that provides a good example of the interdependencies built into rainforest ecosystems. It migrates seasonally from mid-elevations in Parque Braulio Carrillo to lowland areas in the Zona and La Selva. The emerald toucanet is considered one of the more selective frugivorous birds and is attracted to trees in the Lauraceae that are abundant in the upper reaches of the Zona and lower elevations of Braulio Carrillo. This bird is likewise an important seed dispersal agent for many tree species in the Lauraceae. This is one example of many that indicate how the habitat destruction of seed dispersal agents (or pollinators) at one elevation can exert long-term effects on floral regeneration and distribution at other elevations.

Reptiles, Amphibians, and Mammals

Harry W. Greene (University of California, Berkeley) was the herpetologist on the expedition. Despite the poor collecting weather, he recorded 17 species of frogs and toads, 11 species of lizards, 15 species of snakes, and 1 turtle. Most of the amphibians and reptiles are among the 125 species known from La Selva, except for *Atelopus varius*, a strikingly colored, sexually dimorphic harlequin frog, and a toad, *Bufo melanochloris*, both typically found at higher elevations than La Selva (Savage 1972, 1980).

Greene also recorded sightings and signs of 18 species of mammals. We frequently heard and saw monkeys during the expedition, including howler (*Alouatta palliata*), spider (*Ateles geoffroyi*), and white-face (*Cebus capucinus*). Carnivore sightings and signs included the kinkajou (*Potus flavus*), coati (*Nasua narica*), and jaguar (*Felis onca*). We also saw tracks of peccaries (*Tayassu*), deer (*Mazama americana*), and tapir (*Tapirus bairdii*) in upper reaches of the Zona (ca. 700 m).

Observations indicated an abundance of native mammals, whose movements did not appear to be seriously affected by the occurrence of large tracts of pasture (1,208 ha). The protection of remaining forests is crucial, however, given evidence that large vertebrate carnivores and herbivores are likely to disappear within a few years with the isolation of even moderately large patches of tropical forest (Frankel and Soule 1981). Further comments regarding species richness in tropical predators of the La Selva Zona area and their role in maintaining overall community richness are examined by Greene (this volume).

Lepidoptera

The butterfly fauna of the Zona was found to be characteristic of the "foothill belt," an extremely rich zone for butterflies that extends along the base of the Atlantic side of the mountains the length of Costa Rica, and in the transition from tropical wet to premontane rainforest. Isidro Chacón recorded approximately 175 species of butterflies (excluding skippers) during the expedition, despite poor collecting weather. His findings included many rare and little-known species (e.g. *Papilio birchalli, Heliconius eleuchia, Eryphanis polyzena, Caerois gertrutis,* and *Morpho cypris*).

Additionally, in only one and a half nights of black lighting at the 350 m base camp, we obtained 36 species of sphinx months (Sphingiidae) and 13 species of giant silkworm moths (Saturniidae), as well as many other species from at least 10 other families. The rare sphingid *Xylophanes libya* was observed in abundance (over 30 individuals), and the spectacular longtailed saturniid, *Copiopteryx semiramis*, was also collected. The giant sphingid *Amphimoe walkeri*, with its foot-long proboscis, was more abundant at the

Cantarrana base camp than at any other site Chacón and Stiles had collected in Costa Rica. For a more detailed account of the findings of the 1983 expedition into La Zona Protectora La Selva, see Pringle et al. (1984).

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ALTITUDINAL MOVEMENTS OF BIRDS ON THE CARIBBEAN SLOPE OF COSTA RICA: IMPLICATIONS FOR CONSERVATION

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Most applications of island biogeography theory to the design of nature preserves assume a relatively sedentary fauna in a fairly uniform habitat. Neither assumption is met in the mountains of the Caribbean slope of Costa Rica, where 20-25% of the forest avifauna engages in pronounced altitudinal movements on a seasonal or daily basis. Species showing seasonal altitudinal migrations are predominantly fruit- or nectar-eaters, while the much smaller number of species making daily altitudinal movements are either strong-flying birds of prey or aerial insectivores. Conservation of these species requires the presence of forest over a wide range of altitudes, rather than a large area at a particular altitude. For many such species, the elevations spanned by the Zona Protectora are a critical part of their altitudinal migration patterns.

Birds have long held special importance for conservationists: because of their wide appeal, they are often effective symbols for efforts to preserve natural habitats, as is the Bare-necked Umbrellabird (*Cephalopterus glabricollis*) for the Zona Protectora campaign. Because their taxonomy and distribution are relatively well known, birds have also supplied most of the data that have permitted the application of island biogeography theory (MacArthur and Wilson 1967, Diamond 1972) to the design of nature preserves (Wilson and Willis 1975, Terborgh 1974; Lovejoy, this volume). These studies and applications have focused on the minimum area required to sustain viable populations over the long term. Habitat corridors between reserves are recommended mainly to facilitate recolonization following local extinction within any given reserve. In all cases, the authors tacitly assume that bird populations are sedentary in a habitat that is relatively uniform in time and space.

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Where temporal and spatial heterogeneity exist in the habitat, the assumption of sedentary bird populations may not apply. Even the most "aseasonal" wet tropical habitats show pronounced seasonal cycles in flowering, fruiting, and leaf fall (e.g. Medway 1972, Frankie et al. 1974, Stiles 1978, Hilty 1981) and in the activities of the avifauna (Fogden 1972, Stiles 1980 and included references). Local shifts in resource distribution should occur regularly in such communities, favoring local movements of many birds (e.g. Stiles 1980). If the area of interest includes a gradient of elevation or humidity, such local shifts often tend to be oriented along the gradient, and may take the form of regular seasonal movements. The more extensive and widespread are such movements, the more complicated becomes the problem of setting aside preserves for such an avifauna. Area *per se* is no longer the most critical requisite of an effective preserve; adequate representation of the different habitats and resources is also important, and habitat corridors between different areas may be crucial in allowing the birds access to resources.

Except for the vast Amazonian lowlands, mountains represent a dominant feature in neotropical geography, and altitudinal movements might be widespread in this richest of the world's avifaunas. Unfortunately, information on altitudinal movements of these birds is scarce and largely anecdotal. The only comprehensive, quantitative study of altitudinal distribution in the neotropics is that of Terborgh (1971, 1985; Terborgh and Weske 1975). Because his work in the Peruvian Andes was conducted at a single time of year, he was unable to detect seasonal shifts. In Costa Rica, altitudinal migrations of the Bare-necked Umbrellabird and Three-wattled Bellbird (*Procnias tricarunculata*) were described by Carriker (1910), and altitudinal movements were inferred by Slud (1960) to explain seasonal changes in abundance of certain species at Finca La Selva, in the Caribbean lowlands. However, no systematic attempt to evaluate the importance of altitudinal migration in the avifauna as a whole had been made prior to the present study. Such an evaluation could be an important element in designing effective conservation measures for Costa Rican birds, particularly with respect to preservation of the corridor provided by the "Zona Protectora La Selva."

METHODS

Over the past 15 years, I repeatedly visited a number of sites at different elevations on the Caribbean slope of central Costa Rica (Table 1). For each of these visits I compiled a list of bird species present at the site, with supplemental information on the abundance, habitat choice, and behavior of as many species as possible. For purposes of the present study, I have chosen to analyze data for seven sites, separated by 300-600 m and spanning

TABLE 1. STUDY SITES ON THE CARIBBEAN SLOPE OF CENTRAL COSTA RICA, WITH THEIR ECOLOGICAL CHARACTERISTICS AND RESIDENT AVIFAUNAS

Site	Mean Elevation (m)	Location[a]	Life zone[b]	*Resident Avifauna* breeding species	seasonal residents[c]	winter residents
Finca La Selva	100	CC (base)	Tmh	179	32	24
Carrillo	550	CC	Pmh	159	33	21
La Montura	1050	CC	Pp	138	41	18
Muñeco	1550	CT	Pp	114	30	16
Cerro Chompipe	2100	CC	MBp	76	24	12
Río Angeles	2400	CT	MBp	68	23	8
Villa Mills	3000	CT(crest)	Mp	43	22	4

[a] Mountain ranges: CC = Cordillera Central; CT = Cordillera de Talamanca. These two ranges approach each other closely (within 15 km) in Central Costa Rica.

[b] Life zones according to the system of Holdrige et al. (1971): Tmh = Tropical wet; Pmh = premontane wet; Pp = premontane rain; Mbp = Lower montane rain; Mp = montane rain forest.

[c] Seasonal residents = altitudinal migrants present part of each year.

an altitudinal gradient of 100 to 3000 m. The sites do not represent a true altitudinal transect, being situated partly on the Cordillera Central and partly on the northern end of the Cordillera de Talamanca. However, these ranges have similar vegetation and life zones (Tosi 1969) and differ by only about 1% in their avifaunas (cf. Slud 1964). There is also no indication in my data that altitudinal distributions and movements of birds differ between adjacent parts of the two ranges; therefore, I feel justified in provisionally considering these sites as a reasonably close approximation to a true transect.

To facilitate analysis, I compare the avifaunas of these sites with respect to four months of the year: February, May, August and November. In February the dry season is at its height; relatively few birds are breeding except for some hummingbirds, raptors, and hole-nesters. May, early in the rainy season, represents the peak of breeding for a wide variety of species; by August most species have finished breeding and are undergoing their annual molt. November, late in the wet season, is a time of little breeding and molting activity for most species, the major exception being many hummingbirds, whose peak of nesting is in November and December. Migrants from North America are common to abundant in November and February, but present only in small

numbers if at all in May and August. I avoided including the peak months of fall and spring migration (September-October and March-April respectively) specifically to eliminate confusion between latitudinal and altitudinal movements.

I further restricted my analysis to species found regularly or exclusively inside undisturbed forest or along natural breaks in the forest such as treefall gaps, streams, etc. I have excluded species that were not consistently present for most or all of the month in question, thus excluding transient migrants, vagrants, and strays, as well as species dependent upon disturbed habitats. Waterbirds were included only if they depend specifically upon forest watercourses. I excluded a number of wide-ranging species (some swifts and vultures) that fly and forage widely over forest, but are not dependent upon forest for food or nest sites. For the purposes of this analysis, I consider a species to be an altitudinal migrant if it shows a pronounced decrease in abundance at one altitude, at the same time that it shows a roughly corresponding increase at a different altitude. Apparent increases or decreases at a given altitude are not taken as evidence of migration if no reciprocal change is detected at another elevation. This measure of altitudinal migration is certainly indirect, but it is most likely conservative since many movements over short distances or involving only part of a species population would likely go undetected. I consider a species to be an altitudinal wanderer if it regularly moves over a wide span of elevations on a daily or seasonal basis, but does not show any pronounced seasonal shift of the entire population. Finally, the most difficult group to classify consists of those species of which scattered individuals appear, more or less regularly and at a particular time of year, well beyond their species' normal altitudinal range. For species of the first two categories, it is evident that altitudinal movements are fundamental to their way of life, and that the presence of at least sizeable, usually interconnected patches of forest over a wide range of altitudes is essential. For the species in the third category, the importance of altitudinal movements is uncertain. For the present I consider them "altitudinal vagrants" and do not treat them in the analyses, but further studies may show some of them to be true altitudinal migrants.

The baseline for comparing sites, or different seasons at a single site, is the number of species known or strongly suspected to breed at the site(s). Departures of breeding residents and arrivals of nonbreeding residents are summed to give the degree of variation in numbers of species around this baseline. For purposes of this discussion, I consider a species to be resident at a site during a given month if most individuals are present for most or all of the month, and/or there is no indication of transience (e.g. flocks, wide daily fluctuations in numbers, etc.).

RESULTS

General Features of the Avifauna

A total of 548 species of birds has been observed at the seven localities of this study. Of these, 345 qualify as permanently or seasonally resident forest birds, and will be included in the analysis (the complete list will not be presented here due to space limitations, but may be requested from the author). This resident avifauna can be divided into three categories at each site: (a) species that nest at the site; (b) species that nest elsewhere on the Caribbean slope but are seasonally resident; and (c) seasonal residents breeding outside Costa Rica, i.e. migrants from North America. The numbers of breeding and winter resident forest bird species show a linear decline with increasing elevation (Table 1). In order to quantify altitudinal change in the food habits of the avifauna, I established five general diet categories: (a) large vertebrates and carrion; (b) small arthropods (insects, spiders, etc.); (c) large insects and small amphibians and reptiles (since practically every bird that takes one takes the other); (d) nectar; and (e) fruits and seeds. A given species was classified according to its principal food, that to which its morphology and behavior seem to be adapted: thus hummingbirds, which all consume small arthropods, are classified as nectarivores. Many species with mixed diets were classified half in one category, half in another (e.g. those taking large quantities of both fruit and insects, like some motmots or tanagers). I prefer to avoid a heterogeneous "omnivore" category.

Among the birds that breed at different elevations, several well-defined tendencies are evident with respect to diet (Table 2): the proportion of frugivores increases by 37%, and that of nectarivores increases by 50% with elevation, while large insect–small herp eaters and consumers of large vertebrates both decline by over 50%. At all elevations, about 40% of the avifauna consumes small insects and spiders.

Seasonal Changes and Altitudinal Movements

In all seven localities there is considerable variation in the number of resident species over the year (Fig. 1). Leaving aside the winter residents (i.e. those species that breed in North America), the general tendency is for greater numbers of species at low elevations (La Selva and Carrillo) in August and November with the lowest number of species present in May (the main breeding season). At the middle elevations (La Montura and Muñeco), there are more resident species in May and August than in February, with the fewest in November. At elevations above 2000 m, the largest numbers of species are present in February and May, with the lowest numbers in November. It is noteworthy that the curves for the low-elevation sites are virtually

TABLE 2. PROPORTIONS OF DIFFERENT DIET GROUPS AMONG BREEDING FOREST BIRDS OF DIFFERENT ELEVATIONS ON THE CARIBBEAN SLOPE OF CENTRAL COSTA RICA

Locality and Elevations	*Nos. of species/proportions of breeding species feeding on:* Large Vertebrates	Small herps, Large insects	Small Insects	Nectar	Fruits and Seeds
La Selva (100 m)	20 (.11)	28 (.16)	69 (.39)	15 (.08)	48 (.27)
Carrillo (550 m)	16 (.10)	19 (.12)	64 (.40)	14 (.09)	46 (.29)
La Montura (1050 m)	11 (.08)	13 (.09)	59 (.43)	13 (.09)	42 (.30)
Muñeco (1550 m)	8 (.07)	9 (.08)	49 (.43)	10 (.09)	38 (.33)
Cerro Chompipe (2100 m)	5 (.07)	5 (.07)	32 (.42)	7 (.09)	27 (.36)
Río Angeles (2400 m)	4 (.06)	4 (.06)	29 (.44)	7 (.10)	24 (.35)
Villa Mills	2 (.05)	2 (.05)	18 (.42)	5 (.12)	16 (.37)
r_S[1]	-.991**	-1.0**	.696 n.s.	.821*	.964**

[1] Rank correlation (Spearman) between proportion of avifauna in each diet category and elevation. n.s. = $p > .05$; * = $p < .05$; ** = $p < .01$.

mirror images of those for the high-elevation sites in Figure 1. This implies a general downward movement of the highland avifauna following breeding, with a return movement upslope during the dry season.

Variation in the number of resident species through the year is on the order of 6-8% for sites at low and middle elevations, but increases rapidly to 38% at 3000m. The proportion of the species at a site that shows evidence of altitudinal migration increases steadily with elevation (Fig. 2). Nevertheless, a simple count of species present at various sites in different months may underestimate the magnitude of the changes between months, since the departures of some species may be compensated by the arrivals of others. This is especially true of the lower middle-elevation sites, where in fact the largest numbers of altitudinal migrants occur (Fig. 2). When arrivals and departures are considered separately, the true magnitude of the flux through these sites becomes evident, with an excess of arrivals over departures in August, and an excess of departures in November. August and November are the months of most departures at high elevations, and of most arrivals at low elevations (Fig. 3). A 20% turnover of the entire avifauna may occur between some months at middle-elevation sites.

Strong evidence for regular altitudinal migrations was found in 69 species, or 20% of the 345 forest residents of the Caribbean slope. Several representative patterns of altitudinal migration are illustrated in Figure 4. In addition, 19 species qualify as altitudinal wanderers, moving up and down on a more short-term basis, perhaps daily. Virtually all of these species are more or less dependent on having largely or completely intact forest over a wide range

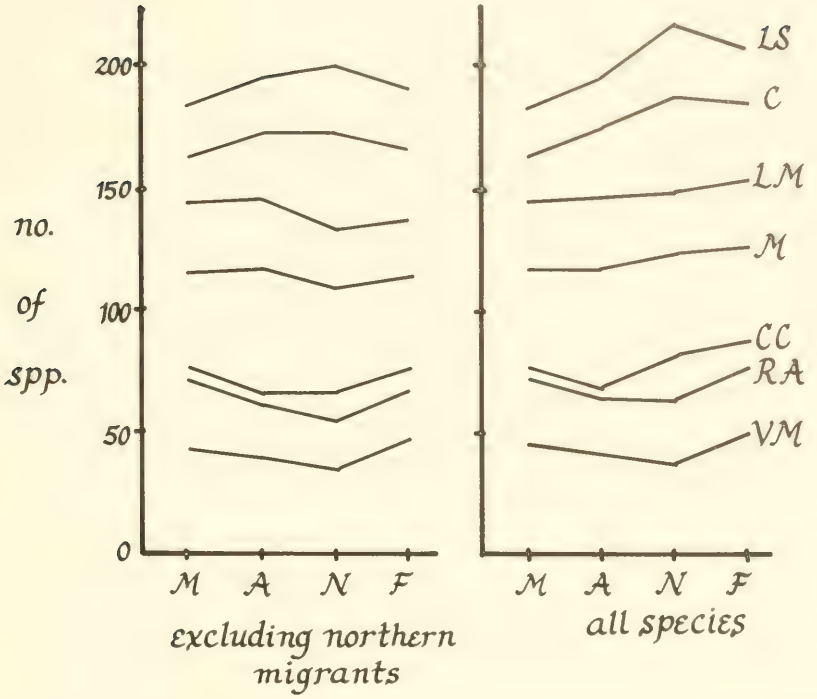

Fig. 1. Seasonal variation in numbers of resident species in sites at different elevations. Sites: LS = La Selva; C = Carrillo; LM = La Montura; M = Muñeco; CC = Cerro Chompipe; RA = Río Angeles; VM = Villa Mills. See Table 1 for site information.

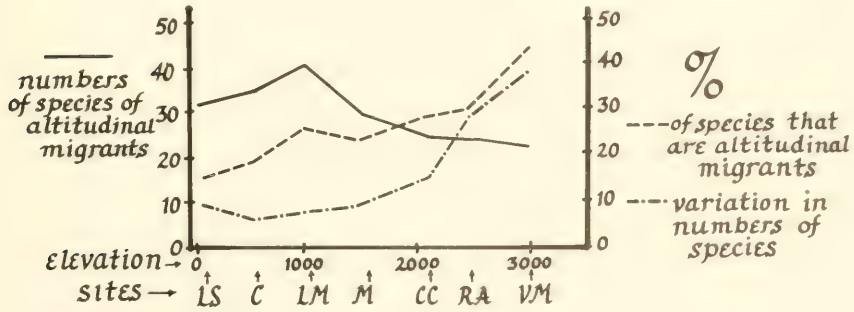

Fig. 2. Variation in the numbers and percent of altitudinal migrants among the resident species at sites at different elevations, and the overall seasonal variation in species numbers at these sites due to altitudinal migrations.

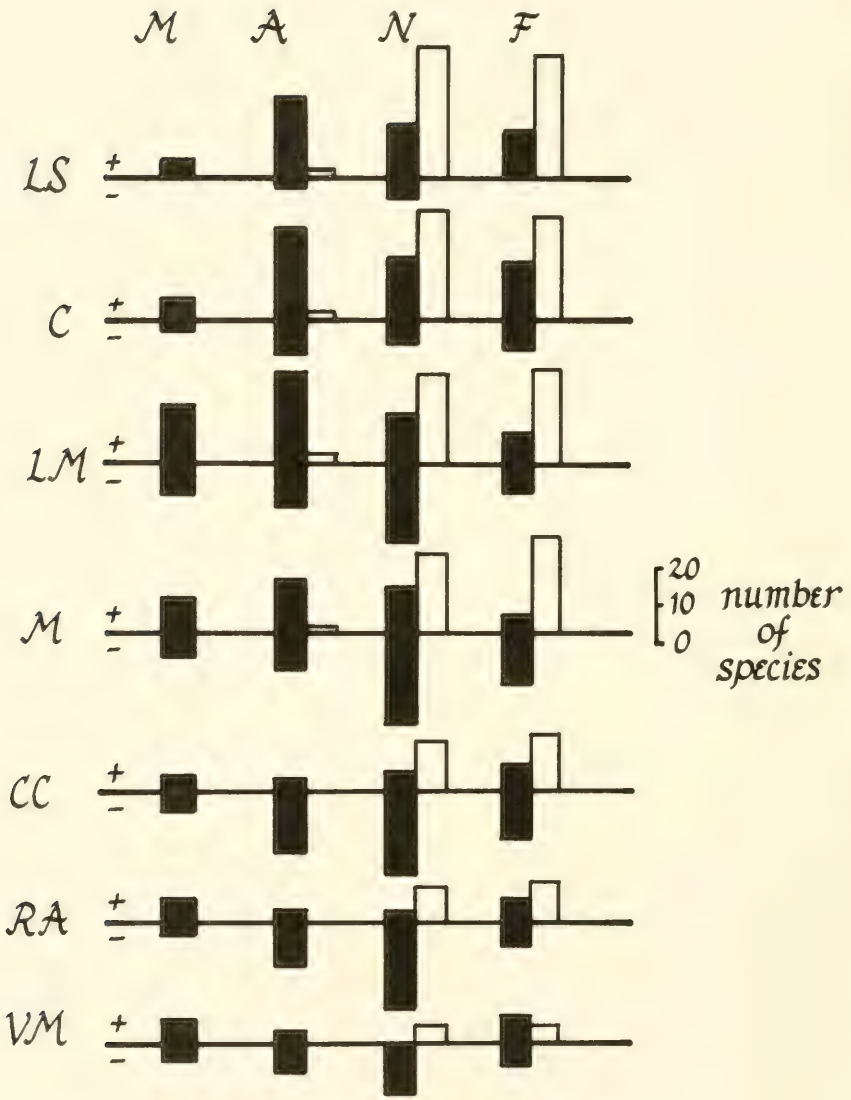

Fig. 3. Seasonal arrivals and departures of resident species at sites at different elevations + (above line) = non-breeding species present; - (below line) = breeding resident absent. Solid bars = tropical species; open bars = northern migrants (winter residents). Abbreviations for sites as in Fig. 1.

of elevations. Also, there are at least 17 additional species that engage in altitudinal movements of uncertain magnitude, at least sporadically. Pending collection of more complete data, these "altitudinal vagrants" will not be considered further, except to note that some may turn out to be true altitudinal migrants.

Altitudinal migrants and altitudinal wanderers do not represent a random sample of the avifauna. Members of the latter group are either aerial insectivores (swifts) or vertebrate-eating kites, hawks, and eagles. Among the altitudinal migrants, relatively more of the frugivores (34%) and nectarivores (56%) on the Caribbean slope are altitudinal migrants than other diet groups, in each of which no more than 20% of the species show such movements (Table 3). Altitudinal migration has a marked effect upon the relation between elevation and the trophic structure of the avifauna; in certain months the trends in diet noted above (Table 2) are totally altered. The increase in the proportion of the avifauna taking fruits with increasing elevation in May turns into a decrease upwards from 1000m in November. Similarly, the increase in nectarivores with elevation is pronounced in November, and scarcely notable in May (Fig. 5). This illustrates a major difference between the hummingbirds and virtually all other groups: the former breed largely at the coolest, wettest time of year, roughly September to December or January, when the greatest numbers of ornithophilous flowers bloom at high elevations (cf. Stiles 1985a, Wolf et al. 1976), and migrate downhill at precisely the time when most other birds are moving in the opposite direction (cf. Fig. 4).

Effects of Winter Residents

Presence of those species breeding in North America is practically restricted to the months of November and February (Fig. 1); by May most have departed, and only one species, the Louisiana Waterthrush, regularly appears in good numbers before the end of August. The numerical effect of these latitudinal migrants is to accentuate the variation in numbers of all residents at low elevations, since their arrival roughly coincides with the arrival of altitudinal migrants from upslope (Fig. 1). In the high-elevation sites, the arrival of these northern migrants partially offsets the departures of many breeding species; moreover, the total number of winter resident species declines notably with increasing elevation (Table 1).

The northern migrants constitute a relatively homogeneous group with respect to diet: nearly all feed principally or entirely on small insects (Table 3). However, some indications of altitudinal movements exist in a few of these species during their residency in Costa Rica.

For instance, Tennessee Warblers and Summer Tanagers reach higher elevations in February than in November (3000m and 2500m, respectively).

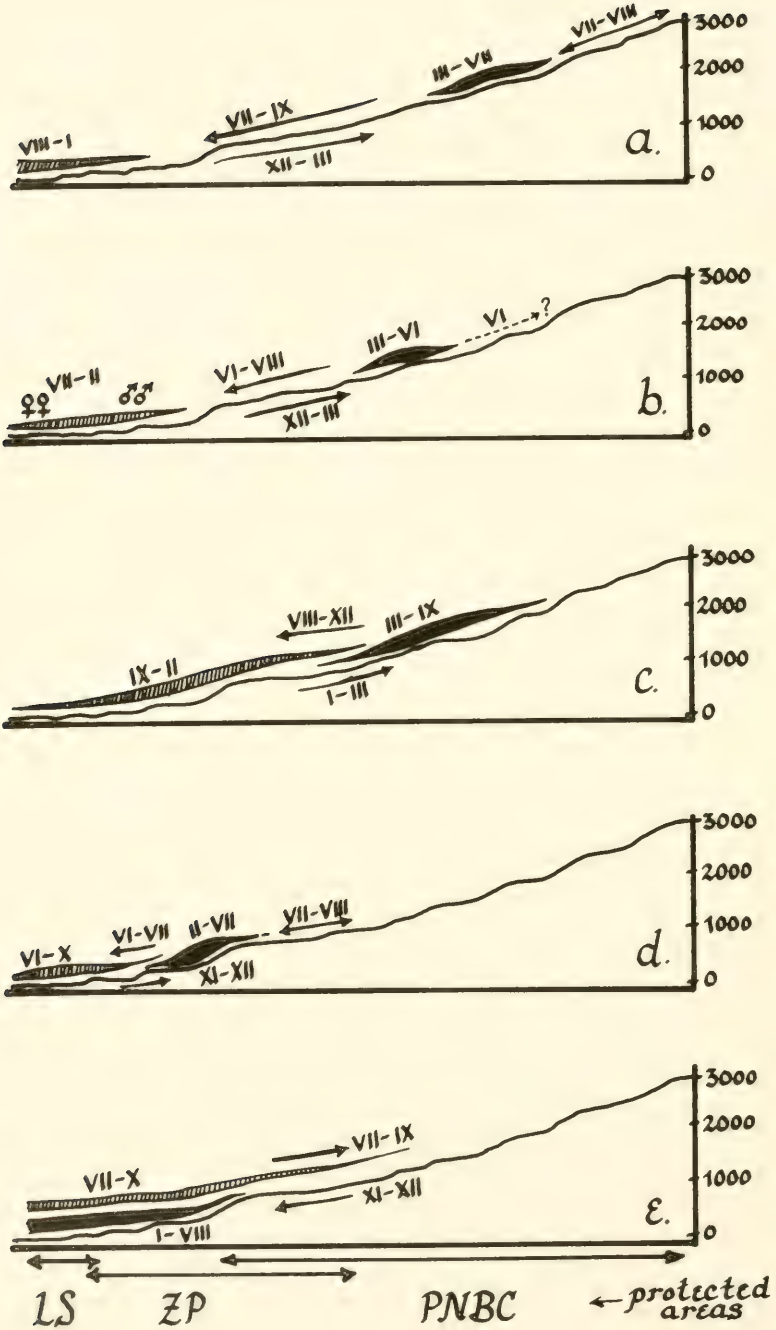
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TABLE 3. FOOD HABITS OF ALTITUDINAL MIGRANTS, WANDERERS, AND VAGRANTS COMPARED WITH THOSE OF SEDENTARY TROPICAL AND WINTER RESIDENT SPECIES[a]

	Large Vertebrates	Small herps and large insects	Small insects	Nectar	Fruits and seeds	Total
Altitudinal migrants	0	5	14	18	32	69
Altitudinal wanderers	5	1	3	0	0	9
Altitudinal vagrants	0	1	5	7	4	17
Sedentary tropical species	23	40	123	7	58	250
All tropical forest species	28	47	145	32	94	345
Winter residents (breeding in North America)	3	1	24	1	5	34

[a] Comparisons (G-tests) of distributions of species among diet categories: (a) altitudinal migrants and wanderers vs. sedentary tropical species, $G = 48.15$ $p < .001$; (b) winter residents vs. all tropical species, $G = 3.71$, $0.25 < p < 0.50$; 4 d.f.

Fig. 4 (adjacent page). Schematic diagram of altitudinal movements of selected species on the Caribbean slope of Costa Rica. Roman numerals = months. Solid figure = breeding distribution; hatched figure = nonbreeding distribution. (a) Three-wattled Bellbird (*Procnias tricarunculata*); (b) Bare-necked Umbrellabird (*Cephalopterus glabricollis*); (c) Olive-striped Flycatcher (*Mionectes olivaceus*); (d) Snowcap (*Microchera albocoronata*); (e) Crowned Woodnymph (*Thalurania colombica*). Note the importance of the Zona Protectora for each species. Protected areas: LS = La Selva; ZP = Zona Protectora; PNBC = Parque Nacional Braulio Carrillo.

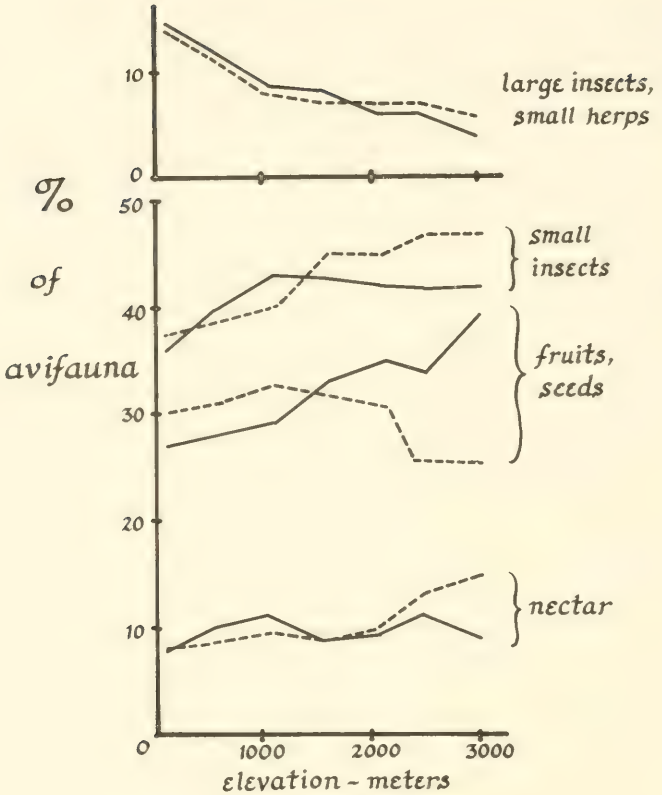

Fig. 5. Changes in the percent of the avifauna taking different foods at different elevations, between May (solid lines) and November (dashed lines). Note in particular how altitudinal trends in proportions of nectarivores and frugivores vary with time of year.

It is noteworthy that the former is the most frugivorous and nectarivorous of the family Parulidae in Costa Rica (cf. Stiles 1983), while the latter is highly frugivorous as well.

DISCUSSION AND CONCLUSIONS

Altitudinal migration has long been known among the birds of temperate-zone mountains, including those of California (Grinnell and Miller 1944). Here, many of the species breeding at high elevations descend to the deserts in winter. Altitudinal migration on tropical mountains has largely been ignored or discounted (e.g. Chapman 1917), perhaps because temperature

changes through the year are negligible. However, the present study has shown that an appreciable proportion, perhaps as high as 25% of the species resident on a tropical elevation gradient, engage in altitudinal movements of some sort on a regular basis. Most of these, including a much higher proportion of nectarivores and frugivores than does the avifauna as a whole, appear to undertake regular altitudinal migrations.

Although rainfall is the major climatic factor driving tropical seasonality, it seems unlikely that the birds showing altitudinal movement are responding to rainfall *per se*: many species do not migrate, and migrations of some species are in the opposite direction from those of others. Rather, most altitudinal migrants seem to be responding directly to changes in the vegetation, specifically the availability of fruit and flowers. Flowering and fruiting patterns reflect rainfall patterns to a considerable degree, of course, but in areas without a strong dry season this relationship is often complex (Frankie et al. 1974, Opler et al. 1980, Stiles 1978). Willis (1966) and others have noted that the resources for many fruit-eating birds are localized, transitory, and often superabundant, and that the birds must be highly mobile to locate new fruit sources as old ones are depleted. Similarly, the patchy, conspicuous, and transitory nature of flowers has favored a high degree of mobility in nectar-feeding birds (Stiles 1973).

The degree of altitudinal movement noted in the avifauna of the Caribbean slope of Costa Rica, if typical of other neotropical mountains, has implications for avian ecology and conservation. It calls into question the conclusions of Terborgh (1971, 1985; Terborgh and Weske 1975) regarding the role of interspecific competition in determining altitudinal limits, since it indicates that for many frugivores and nectarivores such limits are not fixed but vary through the year. Many species of similar diet types show similar movement patterns, rather than opposite, as might be expected were competition *per se* driving these movements. Aggressive behavior and interference competition, while common among nectarivores (Stiles 1973), are exceptional among neotropical frugivores, since fruit is often locally superabundant (Leck 1972, Willis 1966). Clearly, to understand these patterns we need more quantitative local studies of resource availability and utilization (e.g. Wheelwright et al. 1984 for frugivores, Wolf et al. 1976 and Stiles 1985a for nectarivores). For frugivores in particular, such information has wider significance, since the proportion of tree species with bird-dispersed fruits increases with elevation, reaching 70% or more in Costa Rican highland forests (Stiles 1985b). Altitudinal movements of frugivorous birds could not only reflect resource distribution, but influence the distribution of many trees on the gradient.

The implications of these altitudinal movements for bird conservation are clear: on the Caribbean slope of Costa Rica, any preserve that fails to

include a very wide band of elevations, regardless of its size, cannot maintain viable populations of many nectarivorous and frugivorous birds. Many of these species are among the most characteristic and spectacular members of the Costa Rican avifauna. For this reason, the consolidation of the Zona Protectora and the preservation of this forest corridor between the La Selva Biological Station and Parque Nacional Braulio Carrillo is of utmost priority for bird preservation in Costa Rica.

ACKNOWLEDGMENTS

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SPECIES RICHNESS IN TROPICAL PREDATORS

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More than 100 species of vertebrate predators inhabit La Selva, a biological preserve in northeastern Costa Rica. A preliminary analysis indicates that each major feeding guild (e.g. all species that eat birds and bats) includes carnivores, raptors, and snakes, such that a taxonomically focused community study would exclude many potentially important interactions. There are several dietary specialists among La Selva predators, but contrary to previous expectations, a number of species have surprisingly broad diets. High species density is probably due in part to the addition of many species of snakes that eat frogs, to the addition of several species of raptors that eat snakes, and to the addition of raptors and snakes with hunting styles that are rare or lacking in temperate predator assemblages. Circumstantial and experimental evidence supports the view that large predators promote increased community richness, through their controlling effects on populations of smaller predators and herbivores. Predators deserve increased study and recognition as important functional and esthetic components of tropical ecosystems.

The raptors and carnivores of African savannas have inspired numerous books (e.g. Brown 1971; Schaller 1972), and lay people as well as many biologists generally think of that continent as having the richest assemblages of vertebrate predators in the world. In contrast, the high diversity and potential ecological significance of snakes, raptors, and carnivores that eat vertebrates in tropical forests throughout the world have gone largely unmentioned, despite intensive interest in their habitats in recent decades. The primary goal of this essay is to emphasize that the most species-dense predator assemblages are actually found in lowland neotropical forests.

I will describe a team effort to characterize the feeding biology of snakes, raptors, and carnivores of La Selva, an unusually well-studied biological

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station in northeastern Costa Rica. Our preliminary findings on dietary organization of that assemblage suggest a partial explanation for high species richness in tropical predators, and justify some informed speculation on their role in tropical forest ecosystems. With that background, I offer recommendations for the study, conservation, and esthetic appreciation of these animals.

A PREDATOR ASSEMBLAGE IN NORTHEASTERN COSTA RICA

Background and Methods

La Selva is a 7.3 km^2 biological preserve and research station, about 5 km S of Puerto Viejo de Sarapiquí, Heredia Province, on the Atlantic coastal plain of Costa Rica (see Hartshorn 1983 for a detailed description). The full results of our studies will be published as a monographic treatment of the predators of La Selva (Greene et al. in prep.) and several shorter papers on species that were studied intensively (Greene 1986; Greene and Santana 1983; Greene et al. in prep.). Only a synopsis of the methods and results is given here.

The birds of La Selva have been studied since prior to its inception in 1968 as a field station, and the species list for owls and hawks is probably reasonably complete (Slud 1960; Stiles 1983). We obtained information on their prey by direct observation and from literature accounts. For most species we have no new data, but records from elsewhere are sufficient to estimate the diets of many raptors at La Selva.

The list of mammals is based on Wilson (1983), augmented by a record book kept at the station and our observations. Information on the diet of carnivores was gained from scat analyses, direct observation of kills, and literature records.

Scott et al.'s (1983) list of amphibians and reptiles is supplemented by our observations. Information on snake diets is based on palped food items from live animals, field observations of feeding, stomach analyses of museum specimens, and literature records.

A comprehensive review of literature on neotropical predators is beyond the scope of this paper, but important references include Alvarez del Toro (1952; 1971; 1982), Bisbal (1986), Blake (1977), Duellman (1978), Eisenberg et al. (1979), Emmons (1984, 1987), Enders (1935), Greene et al. (1978), Haverschmidt (1962), Henderson et al. (1979), Janzen (1983), Kaufmann (1962), Kiltie (1984), Leopold (1959), Mares and Genoways (1982), Rabinowitz and Nottingham (1986), Schaller (1983), Schaller and Crawshaw (1980), Schaller and Vasconcelos (1978), Seib (1984, 1985), Thiollay (1984), Vaughan (1983), Vehrencamp et al. (1977), Vitt (1980, 1983), Voous (1969), and others cited below.

The Fauna

There are at least 56 species of snakes, about 42 species of raptors, and 14 species of mammalian carnivores at La Selva. Those numbers approximate the total predator assemblage, but they do not describe its exact composition. At least seven species of snakes, eight species of raptors, and four species of mammalian carnivores rarely, if ever, feed on vertebrates. Conversely, known predators on vertebrates in other taxa include at least two bats (*Trachops cirrhosus, Vampyrum spectrum*), a primate (*Cebus capucinus*), an armadillo (*Dasypus novemcinctus*), a peccary (*Tayassu tajacu*), two lizards (*Basiliscus basiliscus, Ameiva festiva*), three frogs (*Bufo marinus, Leptodactylus pentadactylus, Rana warschewitchii*), several nonraptorial birds (e.g. squirrel cuckoo, *Piaya cayana*), spiders, centipedes, and even a katydid (*Copiocera rhinoceros*). Finally, the functional status of some raptors is uncertain, since it is not known if they actually ever feed at La Selva (e.g. *Buteo swainsoni*). Despite these complications in obtaining an exact count, the number of sympatric predators on vertebrates at La Selva clearly is more than 100.

The known snake fauna of La Selva includes 3 boids, 46 colubrids, 3 elapids, and 4 viperids. They range in size from very small (e.g. *Nothopsis rugosus*, less than 10 g) to very large (*Boa constrictor* reaches at least 3 m and 15 kg at La Selva). On the basis of a list of snakes known from the general region (Savage 1980), the total count for La Selva should reach 60 species.

The diurnal raptors include about 35 kites, hawks, hawk-eagles, and falcons. These range in weight from the tiny hawk (*Accipiter superciliosa*, about 75-100 g) to a few species that exceed 1 kg (e.g. ornate hawk-eagle, *Spizaetus ornatus*). The presence or absence of some of these species has varied during the past few decades and certain species are only rarely present (Stiles 1983). Only one raptor, the harpy eagle (*Harpia harpyja*, ca. 4.5 kg; Slud 1960), is known to have been present formerly and now to be lacking permanently from the site. Nocturnal raptors include seven species of owls, two of which are large.

Fourteen species of the mammalian order Carnivora occur at La Selva, including five mustelids, four procyonids, and five felids. These range in weight from the long-tailed weasel (*Mustela frenata*, about 450 g) to the jaguar (*Panthera onca*, to more than 75 kg in Central America). All five cats have been sighted at La Selva within the past five years.

The prey include potentially all terrestrial vertebrates at La Selva: 45 amphibians (1 caecilian, 3 salamanders, 41 frogs), 85 reptiles (1 crocodilian, 4 turtles, 24 lizards, 56 snakes), about 400 birds, and more than 113 mammals. Mammalian prey species weighing 0.5 kg or more include four opossums (*Caluromys derbianus, Chironectes minimus, Didelphis marsupialis, Philander opossum*); howler (*Alouatta palliata*), spider (*Ateles geoffroyi*), and white-

faced (*Cebus capucinus*) monkeys; two sloths (*Bradypus variegatus, Choloepus hoffmanii*), two armadillos (*Cabassous centralis, Dasypus novemcinctus*), and an anteater (*Tamandua mexicana*); a rabbit (*Sylvilagus brasiliensis*); three large rodents, the agouti (*Dasyprocta punctata*), paca (*Agouti paca*), and prehensile-tailed porcupine (*Coendou mexicanus*); brocket (*Mazama americana*) and white-tailed (*Odocoileus virginianus*) deer; collared peccary (*Tayassu tajacu*); and tapir (*Tapirus bairdii*). Among large terrestrial vertebrates, the only prey species known to occur in the past and now lacking in the area is the white-lipped peccary (*Tayassu pecari*; Pringle et al. 1984).

Preliminary Patterns

One of our long-term goals is to prepare a reasonably complete description of the dietary structure of an extremely rich predator assemblage, so that it can be compared in detail with simpler systems. While this is not yet fully possible, certain conclusions are already clear.

First, every feeding guild includes members of each class of predators (a feeding guild is a cluster of predators that overlap signficantly in their use of prey species; see Appendix Note [1]). Among the bird and bat eaters at La Selva are the bat falcon (*Falco rufigularis*) and several other raptors, several species of colubrid and viperid snakes, and perhaps one or more of the small cats (*Felis wiedii, F. yagouaroundi*). A guild of snake eaters contains several diurnal raptors, such as the white hawk (*Leucopternis albicollis*) and semiplumbeous hawk (*L. semiplumbea*); several species of snakes, including the mussarana (*Clelia clelia*) and three coral snakes (*Micrurus* spp.); and one or more mammalian carnivores (e.g. the grison, *Galictis vittata*). Predators on large birds and mammals at La Selva include boa constrictors (*Boa constrictor*) and fer-de-lance (*Bothrops asper*), both large snakes; hawk-eagles (*Spizaetus* spp.), spectacled owls (*Pulsatrix perspicillata*), and other large raptors; and the three largest cats, mountain lion (*Felis concolor*), ocelot (*F. pardalis*), and jaguar. Clearly an attempt to study potential interspecific phenomena, such as exploitative competition for prey and food web structure, might be seriously inadequate if only a single group (e.g. diurnal birds of prey) were studied. This finding echoes the situation in a simpler predator assemblage in temperate Chile (Jaksic et al. 1981).

A second tentative conclusion concerns diet breadth, a topic of interest because it has been suggested that one way more species could be packed into a complex community is by each of them having narrower food niches than in simpler communities (Klopfer and MacArthur 1961). We found that there are indeed some diet specialists among the La Selva predators; coral snakes and the laughing falcon (*Herpetotheres cachinnans*), which feed almost exclusively on snakes; and the bushmaster (*Lachesis muta*), a large viper that

preys primarily on spiny rats (*Proechimys semispinosus* at La Selva).

There are, however, a number of extreme diet generalists among the La Selva predators. These include the eyelash viper (*Bothriechis schlegeli*), which eats frogs, lizards, birds, mouse opossums, bats, and rodents; the fer-de-lance, which takes a variety of invertebrates and small vertebrates; and the jaguar, which eats turtles, crocodilians, iguanas, fish, birds, and a variety of mammals ranging from sloths to peccaries.

It is important to specify whether a narrow diet range means a small number of "kinds" of prey (i.e. those that are similar in size and attributes that are relevant to a predator) or a few species of prey (Greene and Jaksíc 1983). Beebe (1950) recorded 56 species of birds, 14 species of insects, 5 species of bats, and 3 species of amphibians and reptiles among 218 items captured by a pair of bat falcons. Although only a few kinds of prey were eaten, a population of this small raptor has a broad food niche in terms of impact on different prey species populations. If other predators that take more *kinds* of prey than the bat falcon eat comparably more *species*, their total impact in a community is very widespread.

A few examples illustrate a third finding, that the La Selva predator assemblage includes species with hunting styles that are rare or absent in temperate faunas. Nocturnal cat-eyed snakes (*Leptodeira septentrionalis*) eat the arboreal eggs of red-eyed treefrogs (*Agalychnis callidryas*), scraping their chins along leaves until the gelatinous mass is located (Pyburn 1963). Crane-hawks use their unusually jointed legs to search among the axils of bromeliads and crevices in trees for large insects, amphibians, reptiles, and nestling birds (Sutton 1954). Tiny hawks hide near vacant hummingbird perches, then ambush the territory holders when they return (Stiles 1978).

A final generalization from our study is that most vertebrates in tropical rainforests face a bewildering array of potential predators. For example, green iguanas (*Iguana iguana*) of all sizes are eaten by a variety of other lizards, diurnal and nocturnal snakes, raptors and other birds, and mammals (Greene et al. 1978). Spiny rats (*Proechimys* spp.) are often abundant in lowland neotropical forests (Emmons 1982), play important roles in the population biology of some trees (Vandermeer et al. 1979), and are eaten by a variety of snakes and carnivores. The snake fauna of La Selva is sufficiently diverse in terms of habits and morphological specializations that most frogs are probably never free of the threat of discovery. This complexity of predator-prey interactions has important implications. One is that tropical prey species might show antipredator specializations different from those seen in temperate zones (cf. Moynihan 1971; Robinson 1970). Another is that food web theory, which currently focuses on assemblages of no more than about 30 taxa (Pimm 1982), might have to cope with literally thousands of components at a single tropical site if worldwide generality is to be achieved.

ASPECTS OF HIGH SPECIES RICHNESS IN TROPICAL PREDATORS

The numbers of species in most groups of organisms is higher at lower latitudes, and this "species richness gradient" has long intrigued naturalists (Schall and Pianka 1978). Ideally, a comparison of predator assemblages would involve many areas throughout the world, so that detailed contour maps could trace latitudinal and other changes in diversity. This is not yet possible, because the faunal composition of many tropical sites is so poorly known. Although the snakes, raptors, or carnivores have been surveyed at numerous localities, there are only a few places where all vertebrate predators have been documented adequately for comparison with La Selva. Table 1 illustrates an approximately ten-fold increase in the total number of vertebrate predators between depauperate and rich assemblages.

Work thus far implicates historical and abiotic factors as causes of high tropical species diversity (e.g. continental fragmentation, earthquakes, speciation and extinction rates), as well as others that reflect contemporary biotic interactions (Diamond and Case 1986). Within the latter category, more species might coexist by decreasing diet breadth, increasing diet overlap, changing the overall guild structure of an assemblage, increasing the total amount of niche space, or some combination of these parameters (Colwell 1979). There are as yet not enough data to compare patterns of diet overlap among temperate and tropical predator assemblages. The possibility that high species density is influenced by total niche space—that there are more kinds and/or species of prey in the tropics—is explored in this section.

Previous studies established that much of the apparent increase in mammalian species richness in the tropics is due to the enormous increase in bat diversity at low latitudes (Janzen and Wilson 1983; but see Emmons et al. 1983). This finding and direct comparisons with other faunas (Table 1) demonstrate that the order Carnivora is not represented substantially better at La Selva than at some temperate localities. Moreover, as Janzen and Wilson (1983) emphasized, tropical carnivores are sometimes partially or completely frugivorous. Examples at La Selva include a mustelid (*Eira barbara*), at least two procyonids (*Nasua nasua, Potos flavus*), and perhaps others.

Our studies suggest that an important component of the increase in vertebrate predators might be the addition of hawks, particularly those that feed either frequently or always on snakes. Examples at La Selva include the laughing falcon, white hawk, and semiplumbeous hawk. There is also a large increase in numbers of species of snakes in tropical habitats, and at La Selva about half of those feed on frogs. Examples include medium to large racers (*Chironius grandisquamus, Drymobius melanotropis*), a coral snake mimic (*Pliocercus euryzonus*), and several small leaf-litter snakes (e.g. *Amastridium veliferum, Rhadinaea decorata*).

TABLE 1. SPECIES RICHNESS IN TEMPERATE AND TROPICAL PREDATOR FAUNAS [(2), see Appendix for details and sources]

Locality	Snakes	Owls	Hawks, etc.	Carnivores	Total
Arctic sites					
Barrow, Alaska (3)	–	2	2	3	7
Umiat, Alaska (3)	–	1	7	7	15
Temperate chaparral					
Santiago, Chile (4)	2	3	5	1	11
Doñana, Spain (5)	5	3	9	5	22
Hastings, California (6)	10	6	12	11	39
Temperate desert					
Big Bend, Texas (7)	32	10	26	13	81
Tropical savanna					
Kruger, So. Africa (8)	45	10	41	24	120
Tropical rainforest					
La Selva, Costa Rica (9)	56	7	35	14	112
Manu, Peru (10)	ca. 65	8	35	16	ca. 124

In other words, an underlying factor in the increased species richness in neotropical predators is probably the presence of more kinds of frogs than in temperate faunas, particularly members of the diverse and abundant terrestrial genus *Eleutherodactylus*. More than a third of the frogs at La Selva belong to this genus (Savage 1980). By contrast, about 5 to 15 species of anurans would be found at a temperate locality (Conant 1975; Stebbins 1985), including at most, three or four terrestrial species of *Bufo*. This difference in the availability of terrestrial frogs as prey is exacerbated by the fact that *Bufo* spp. have toxic skin and are typically eaten by only a few species of snakes (at La Selva, by *Leptodeira annulata* and *Xenodon rabdocephalus*).

Arnold (1972) demonstrated a statistically significant relationship between species densities of snakes and their vertebrate prey over a latitudinal gradient in North America. The hypothesized effects of increased numbers of frogs and snakes in promoting higher overall predator richness at La Selva is consistent with Arnold's result, but the situation is undoubtedly more complicated than implied by that explanation. Because the evidence is only correlative, one also could argue that high predator diversity promotes high prey diversity. Although that is probably true in part (see next section), it is unlikely to be the whole story (cf. Arnold 1972; Inger 1980). The findings from La Selva suggest that patterns of niche breadth, niche overlap, and guild structure also might be important. In any case, an explanation restricted to

top predators and their prey begs the question of high species diversity in an ultimate sense: why are there more frogs, more insects, and more trees in the tropics? The answer undoubtedly involves matters of climate, history, chronic disturbance, and feedback interactions among the organisms themselves (see Janzen, this volume, and reviews in Diamond and Case 1986).

CONSEQUENCES OF PREDATOR DELETIONS IN TROPICAL FORESTS

The prospects for and potential consequences of predator extinction in northeastern Costa Rica are cause for serious concern. Cattle pasture now borders La Selva on three sides, which is connected by a forest corridor on the south to Braulio Carrillo National Park (Pringle et al. 1984; Clark, this volume). Theoretical and empirical considerations suggest that predators are often particularly sensitive to habitat loss (Terborgh and Winter 1980). Typically these animals are large, have low reproductive rates, are high in food chains, have intrinsically small population sizes, and are especially vulnerable to human persecution for their pelts or because of prejudice. The consequences of habitat fragmentation for large, tropical predators are confirmed by experience on Barro Colorado Island (BCI), Panama. When the hilltop that is now BCI was isolated by completion of the Panama Canal, all large predators disappeared within the first few decades (Eisenberg 1980; Glanz 1982; Terborgh and Winter 1980).

There is theoretical and empirical support for a "predator richness hypothesis," that predators can increase the overall species diversity of a community by depressing the populations of smaller predators and of herbivores. Decreased populations of some smaller predators might permit the coexistence of other herbivores and/or lower their impact on plant populations. Discussions of these effects in non-tropical ecosystems and from theoretical perspectives are found in Paine (1966), MacArthur (1972), and Diamond and Case (1986).

Turning to the tropics, Willis (1974) postulated a relationship between absence of large predators on BCI and the extinction of certain birds. Janzen (1978) suggested that loss of predators could even affect overall forest structure, by permitting larger populations of herbivores. Terborgh and Winter (1980) and Eisenberg (1980) noted that medium and large mammals now live predator-free on BCI, and are more abundant there than those authors observed anywhere else in the neotropics.

Subsequent work is consistent with some of those expectations. Loiselle and Hoppes (1983) demonstrated experimentally that artificial nests were subject to significantly more predation on BCI than at nearby mainland localities. Carr (1982) attributed dramatic decreases in the litter fauna of peninsular Florida during the past four decades to a highly successful invasion

of armadillos and concomitant near-extinction of mountain lions and black bears (*Ursus americanus*). Armadillos are known to eat small vertebrates, even vipers, and Carr (1982) cited recent records of predation by mountain lions and bears on armadillos. Other studies have documented the dramatic direct and indirect negative effects of introduced small and medium size predators on native birds and reptiles in places where there are no larger predators (e.g. George 1974; Iverson 1978).

At La Selva, studies thus far do not bear directly on this issue, but they confirm certain necessary corollaries of the predator richness hypothesis. Our data and published observations demonstrate that large predators do kill smaller predators: in addition to other prey, forest falcons (*Micrastur* spp.) eat coral snakes and screech owls (*Otus guatemalae*); bird snakes (*Pseustes poecilonotus*) eat bat falcons; harpy eagles take coatis (*Nasua nasua*) and tayras (*Eira barbara*); boa constrictors eat coatis and ocelots; and jaguars feed on armadillos, coatis, ocelots, and raccoons. Predators also eat large herbivores, including a substantial number of sloths and iguanas at La Selva.

Glanz (1982) criticized the predator richness hypothesis as purely speculative; he suggested that the apparent high densities of some mammals on BCI are either caused by forest characteristics other than predators or based on an observational error. Leigh (1982) went farther in stating matter-of-factly that available evidence suggests that herbivore populations on BCI are not predator limited. Nevertheless, several observers with wide experience studying mammals in tropical forests consider the BCI situation noteworthy, and both observations and experiments indicate that nest predation there is significantly higher than elsewhere. Glanz' cautionary remarks are well taken but, given the available evidence, the reality of the predator richness phenomenon seems more likely than not. Leigh's statement is simply incongruous, because there are no longer predators on BCI that *could* regulate the large herbivores!

It is worth emphasizing that worldwide, heavy human impact on predators has not been restricted to that by Westerners in the 20th century (cf. Lopez 1986: 337; Myers 1973; Schueler 1980). As a result, current densities of snakes, raptors, and carnivorous mammals, especially large species, are surely well below maximum levels in many places. Any ecosystem-level consequences of their presence must be less than those effects would be under pristine conditions, perhaps far less.

RECOMMENDATIONS

Our studies and those of others document the presence of rich predator assemblages in neotropical rainforests. La Selva has approximately 100 sympatric predators, more than are known for any other site of comparable size and as many as ten times the number present at some temperate localities.

Manu National Park in Peru is much larger and not as completely surveyed as La Selva, but based on studies by Dixon and Soini (1976) and Terborgh et al. (1984), that general region of western Amazonia probably harbors the most diverse predator fauna in the world (Table 1).

The devastation of tropical forests is a grave international problem, and lasting solutions must encompass complex sociopolitical issues as well as basic questions in ecology (see Simberloff 1985, and papers by Gamez and Ugalde, Gomez, and Raven, this volume). We cannot ask Latin Americans to save wild cats and dangerous snakes for the sake of ideals that may seem strange and extravagant to local people. Whatever the benefits of saving the corridor from Braulio Carrillo to La Selva, they must be seen as meaningful to Costa Ricans. The following recommendations, although focused on vertebrate predators, are intended for that context.

(1) The preparation of detailed faunal inventories is a critical initial step in conservation and management. It is sometimes claimed that vertebrate faunas are known thoroughly in most areas, but this is simply not true for tropical regions. Very few sites exist for which even approximate lists of all vertebrates can be prepared, and I know of none for African or Asian lowland forests. The problem is exemplified by the situation in northeastern Costa Rica. Although La Selva was already one of the best studied tropical localities when we began to work there, eight species of snakes were added to the known fauna within three years. A few miles away, the first biological reconnaissance of the Zona Protectora discovered a lizard and birds that were previously unknown from Heredia Province (Pringle et al. 1984).

Although collecting certain species can no longer be justified, series of most vertebrates should be obtained in the most technically modern context possible (e.g. photographs, tissue samples, extensive field notes, as well as traditional preparations), then deposited in established museums for permanent curation and further study. It seems especially important that body weight, stomach contents, reproductive condition, and microhabitat be noted if animals are collected for museums, something that has been surprisingly infrequent in the past. Recent studies of Asian herpetofauna by Inger (1980) and of neotropical birds by the Louisiana State University Museum of Zoology (e.g. Parker et al. 1985) are exemplary in that regard.

(2) We are abysmally ignorant of the natural history of most tropical predators, such that autecological work on all species is still needed. Even an animal as widespread as the boa constrictor has never been subjected to a detailed field study (cf. Greene 1983). In terms of potential ecosystem impact, this lack of knowledge is particularly severe for raptors and small carnivores. Only a few tropical falconiforms are even marginally well known in terms of diet, and then only from studies on a few nesting pairs (e.g. bat falcon, Beebe 1950; harpy eagle, Rettig 1978). Virtually nothing is known about the

behavioral ecology of the jaguarundi (*Felis yagouaroundi*), a cat that ranges from the southwestern United States to temperate South America.

(3) The predator richness hypothesis deserves further attention, but it will be difficult to test experimentally with tropical vertebrates. Perhaps controlled removals and additions of predators could be performed, using small islands or the Brazilian forest plots under study by Lovejoy et al. (1984). It even might be feasible to reintroduce one or more large cats onto BCI, such that possible effects on the densities of smaller predators could be examined. Another approach would be "natural experiments" (cf. Diamond 1986), in which replicate sets of faunas are examined systematically for the presence and absence of predators with respect to each other and to prey species richness (e.g. Arnold 1972).

The difficulties of working experimentally with predator assemblages are countered by certain advantages. They vary in species richness, from Poles to the Equator, by a factor of more than ten. Vertebrate prey usually can be identified to the generic or specific level, thus permitting precise calculation of niche breadth and niche overlap (Greene and Jaksíc 1983). Because vertebrate predators and prey have relatively good fossil records, there also is the intriguing prospect of synthesizing paleontological, functional, and ecological data (e.g. Andrews et al. 1979; Radinsky 1981; Van Valkenburgh 1985).

(4) Given the general level of ignorance that prevails with regard to predators and their potential significance in tropical ecosystems, it is important not to ignore or abandon these animals. This means that management plans for any region large enough to include conceivably viable populations should strive for their continued existence. "Conceivably viable populations" must be stressed here, for pragmatic reasons. We lack solid data on the home range size and densities of most species, so "rules" for minimum population size are not applicable (Soule and Simberloff 1986). Furthermore, the esthetic and ecological benefits of predators might warrant the artificial maintenance of small, "subviable" populations (e.g. by periodic introduction of transplanted or captive-bred individuals.)

A second management consideration involves the inevitable risks associated with chasing, anesthetizing, and radio-tracking large vertebrates. Until there is firm evidence that populations of these animals are not in jeopardy, specifically cats and tapirs in northeastern Costa Rica, research that might harm them should be discouraged. The potential risks sometimes can be justified in very large preserves in order to acquire information that is important for long-term management, but not in an area as circumscribed as La Selva and the Zona Protectora. Alternatives include the use of non-disruptive methods (e.g. identifying individuals by unique track characteristics, L. H. Emmons, pers. comm.), and extrapolation from studies at other sites.

REFLECTIONS

The above suggestions imply revised attitudes toward tropical predators, in terms of basic research and ecosystem management. Progress in conserving predators also will require educational efforts that emphasize their diversity and potential ecological significance, with the goal of enhancing the esthetic appeal of these animals. Carnivores and raptors are appreciated to some extent, of course, but traditionally it is only the large, showy, and easily observed species that have attracted attention.

We are never going to be able to drive a van, painted like a paca and bristling with camera lenses, into a lowland tropical forest and show the tourists a quick jaguar. Instead, we need to cultivate a perspective such that walking in a forest inhabited by predators is *different* than walking in a forest that lacks them, even if one doesn't see any cats or hawk-eagles on that particular day. This goal should be achieved without recourse to excessive sentimentalism and anthropomorphism, attitudes that characterize too commonly our modern views of other creatures. An esthetic appreciation of tropical predators should stress instead the unique specializations of each species as well as their reciprocal interactions with other organisms, even those as "lowly" as small brown frogs. This appreciation need not exclude a feeling for the beauty and controlled power of predators, and could profit from a grounding in ancient and worldwide traditions of awe and respect (e.g. Lathrop et al. 1975; Lopez 1978; Wilson 1984). It almost goes without saying that I disagree strongly with the sad and naive claim that predators are no less than evil incarnate (e.g. Skutch 1980). Toward that goal, I'll close by recounting some experiences with these animals at La Selva.

As a Costa Rican friend said, "Todo el mundo quiere ver un tigre"—everybody wants to see a jaguar. Few people meet tropical cats in the wild, but there are occasional sightings of the five species at La Selva. An insect ethologist was squatting on a trail late one night, looking at cockroaches, when she sensed a nearby movement on the boardwalk and looked up to see a big jaguar watching her from a few feet away. Tales of such dramatic encounters can prime one for the forest, but seeing a jaguar cannot be anticipated fully.

For me, it was nine months of examining tracks, one set of them beside a stream and so fresh that water was still seeping into the pug marks. It was picking up dozens of scats and puzzling over their contents, the drab record of lives briefly met (Fig. 1). Sometimes I marveled over a protruding, intact sloth claw, and sometimes the droppings were so fresh I wondered if the flies had just arrived. Once a botanist lead me to a fresh kill, the shell and a few other bloody remnants of a large armadillo. It was fleeting shadows and

Fig. 1. Remains of a young collared peccary (*Tayassu tajacu*) and a two-toed sloth (*Choloepus hoffmanni*), both recovered from a single scat of a jaguar (*Panthera onca*).

strange sounds, most of which were birds or something else, and always hoping but never expecting to see the cat.

One night three of us were walking up a muddy trail, listening to frogs and watching for snakes in the understory. Craig Guyer said abruptly, "Hey, a cat!" It had bounded once on the trail in front of him and vanished. We swung our lights into the trees and saw the hind quarters of a jaguar about 10 meters away. After a second or two, it stepped into full view among the leaves. A young animal, all spots and long tail, it squinted briefly at us before melting silently into the darkness. Everything in our collective lives said that cat had not *actually* dissolved, but I now understand better why aboriginal people attribute mystical qualities to forest creatures.

A bushmaster was sighted crawling slowly through the forest at dawn, a few meters outside the laboratory clearing at La Selva. At almost two and a half meters in total length and three kilograms in weight, it was only an average-sized adult of the world's largest viper. A dozen or so people soon gathered in a respectful circle, rapt observers. The snake lay extended and still, with its head cocked slightly to one side. Occasionally its black tongue draped rhythmically, sampling the remaining fog and trying to get a feel for our relevance in its morning. Among the group were doubtless some who grew up with the prejudices that threaten snakes everywhere, and in a different situation some of them would have been genuinely frightened to the point of panic. All such concerns were forgotten that morning, and eventually the bushmaster began to crawl slowly toward a nearby tree buttress. Someone pointed out how difficult it was to see the alternating black and brown pattern against the leaves and other litter of the forest floor, a fact that was all the more impressive given the snake's size. A Costa Rican mentioned the local name "matabuey," and wondered if it really could "kill an ox." Everyone knew that few people have seen this species in the wild, that we were privileged.

The snake behind the lab clearing was one of 15 bushmasters I've seen, and with Manuel Santana I followed some of the others for weeks on end, long enough to begin to learn something about their lifestyle. We documented a cycle of nocturnal ambush hunting and daytime sleeping, part of a larger pattern of irregular and infrequent movements between hunting sites. Our studies also disclosed that bushmasters require only a few, relatively large meals each year to support the energetic costs of their sedentary hunting tactics (Greene and Santana 1983).

Early that morning, squatted down and watching the bushmaster at almost ground level, I was drawn to its head and the battery of senses aimed at me. A pit viper has two nostrils and a slowly wavering tongue that serve chemoreceptive functions, and two dark eyes with tight vertical slits for pupils—all senses we can at least imagine because we share those modalities. There are also two pits, one on either side of the head between eye and nostril, that are extremely sensitive radiant heat receptors. A recent and remarkable finding is that receptor endings in the pits are mapped spatially on the optic tectum of the brain, so that these snakes presumably "see" their prey as superimposed infrared and visual images (Hartline et al. 1978).

Knowledge about ecology and neurobiology enhances my appreciation for animals, but it also provides a more subtle and paradoxical reward. Looking into the bushmaster's face, those eyes and pits and nostrils and that solitary black tongue, we confront a deep mystery. There is an unbridgeable gap, where our senses meet that snake's pits and science gives way to art. It is inconceivable that reductionistic molecular biology, despite all of its acknowledged power and much-deserved acclaim, can fathom fully that barrier.

Sooner or later, whether campesino or bird watcher or visiting herpetologist, we *need* that kind of profound mystery, and it will persist as long as there are jaguars, white hawks, and bushmasters in tropical forests.

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This essay is dedicated to the memory of Len Radinsky (1937-1985).

APPENDIX

(1) Root (1967:335) defined a guild as "a group of species that exploit the same class of environmental resources in a similar way." I follow Jaksíc (1981) and MacMahon et al. (1981) in de-emphasizing the "in a similar way" part of that definition for community-level phenomena, where the key point is whether self-renewing populations are affecting each other. If two predator species eat the same prey species, in terms of interspecific effects, it matters not whether they are both nocturnal, arboreal, etc. The guilds in this paper are defined tentatively and broadly for now, and further study will undoubtedly partition them to some extent. Nevertheless, I expect that their apparent taxonomic complexity is real.

(2) These figures could be modified to reflect historic fluctuations and the fact that some species undoubtedly feed largely or entirely on invertebrates or plants. All of the temperate sites and Kruger Park are larger than La Selva and more topographically diverse, so that no 7.3 km^2 portion of those localities would yield species counts as high as those listed here. By contrast, a Costa Rican "plot" as large as Big Bend National Park would yield many more species of predators than are found at La Selva, and the increase would be caused mainly by the addition of snakes (cf. Savage 1980).

(3) Barrow (71 deg. 17 min. N) is tundra, Umiat (69 deg. 22 min. N) is foothills, and both are based on F. A. Pitelka (pers. comm.). The figures

under "hawks, etc." include non-raptorial birds (e.g. jaegers) that eat vertebrates.

(4) Two nearby localities, forming a 36.5 km^2 preserve (33 deg. 22 min. S), based on Jaksíc et al. (1981).

(5) An 87.6 km^2 preserve (36 deg. 30 min. N), based on Valverde (1967).

(6) A 7.7 km^2 Natural History Reservation (36 deg. 23 min. N), based on Davis et al. (1980), Grinnell et al. (1937), and unpublished records on file at the reservation. These totals include the grizzly (*Ursus horribilis*), which was common in coastal California until recently and is now extinct in the state.

(7) A 1600 km^2 National Park (29 deg. 30 min. N), based on Wauer (1980).

(8) A 10,715 km^2 National Park (centered on 24 deg. S), based on Pienaar (1964, 1966, 1969) and Pienaar and Prozesky (1961, 1967). The numbers for raptors include taxa that had only been sighted once in the park, so there are fewer functionally significant species than listed, for that reason as well as others cited above (2).

(9) A 7.3 km^2 Biological Station (10 deg. 26 min. N), based on our studies and those of others (see text).

(10) A small Biological Station, within an 8615 km^2 National Park (11 deg. 55 min. S). Based on Terborgh et al.'s (1984) survey of Cocha Cashu, and on Dixon and Soini's (1976) account of snakes of the Iquitos region.

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PRELIMINARY DESCRIPTION OF PRIMARY FORESTS ALONG THE LA SELVA-VOLCAN BARVA ALTITUDINAL TRANSECT, COSTA RICA

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The La Selva-Volcán Barva altitudinal transect includes four ecological life zones and two significant transitional zones. Tropical premontane rain and tropical lower montane rainforest life zones comprise 75% of the park complex, whereas tropical wet forest life zone (including cool transition) covers only 13% of the Braulio Carrillo complex (including La Selva). The changeover between any two life zones or transitions occurs over an altitudinal range of 100-300 m.

Seven types of primary forests are characterized floristically and physiognomically. Many tree species occur not only in more than one forest type, but also in more than one life zone. The frost line (1300-1600 m) is the most striking floristic change along the altitudinal transect. Detailed mapping of landforms and forest types on two 1.0-km^2 plots demonstrates strong topographic control and gradual change between adjacent forest types.

In contrast to the appreciable amount of ecological information available about La Selva (cf. Janzen 1983), very little is known about ecosystems in the Peje Sector of Braulio Carrillo National Park (PNBC). The first scientific information on the Peje Sector (Pringle et al. 1984) came from a brief OTS expedition to the lower La Selva Protection Zone (ZP). Study sites along the altitudinal transect were established in 1985 as part of Operation Raleigh's comparative investigations of tropical rainforest in Costa Rica, Cameroon, and Indonesia. Primary forests along the altitudinal transect were used in a 1985 NASA project to map ecological life zones (Holdridge 1967) and to characterize the structure, composition, and distribution of forest types. The authors' involvement with Operation Raleigh and the NASA project forms the basis of this first attempt to characterize primary forests along the altitudinal transect between La Selva and Volcán Barva.

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STUDY AREA

The La Selva-Volcán Barva transect (Fig. 1) spans an altitudinal range of nearly 3000 m over a map distance of about 35 km. Volcán Barva (2906 m) is part of the Cordillera Volcánica Central that frames the northern side of the populous Central Valley. By means of a new highway to Guápiles in the Caribbean lowlands, the southern boundary of Braulio Carrillo National Park (Boza and Mendoza 1981) is only a 20-minute drive from downtown San José, the capital of Costa Rica.

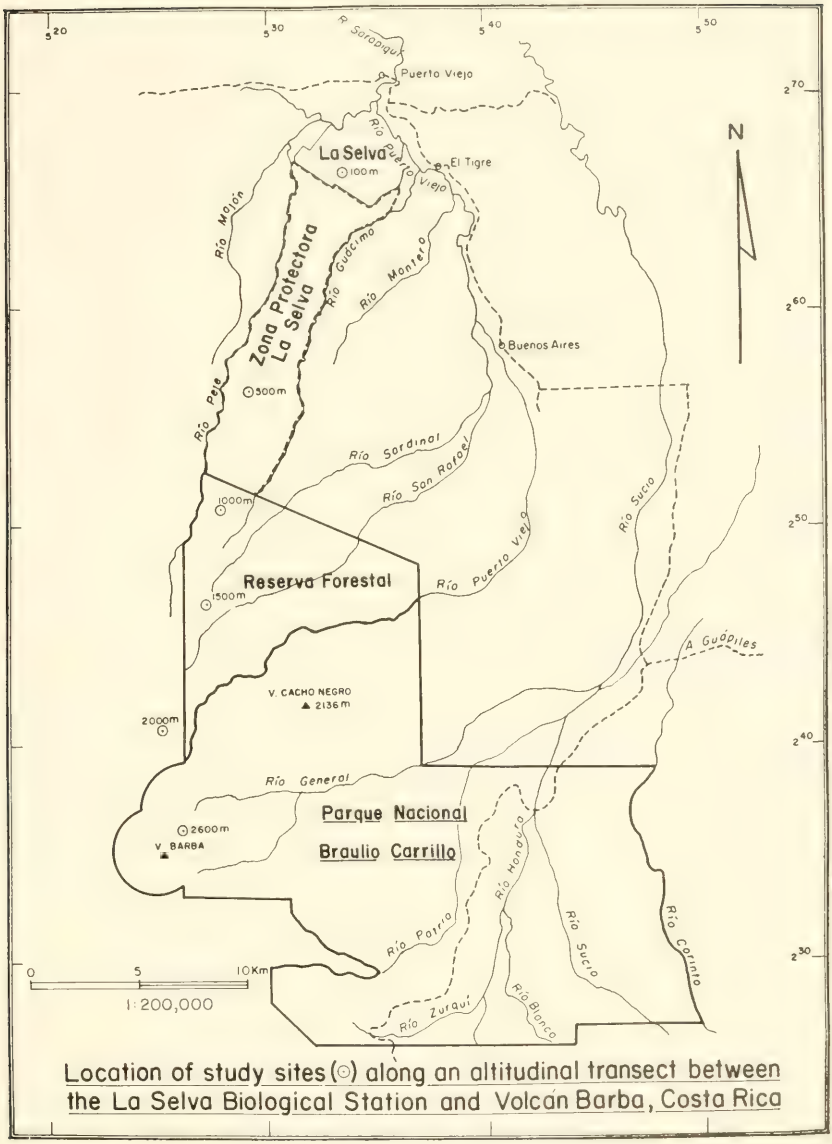
North of Volcán Barva are some satellite volcanoes (e.g. Cacho Negro), calderas, and lava flows. One of the lava flows underlying the La Selva Biological Station is dated at 1.2 million years BP. Costa Rican vulcanologist Guillermo Alvarado (pers. comm.) has identified the remnants of an unknown caldera north of Volcán Barva, hence the source, age, and extent of the principal lava flows of the Peje Sector of PNBC are uncertain. Though the north-south slopes of the transect are moderately gentle (averaging 4°; G. Alvarado, pers. comm.), the lava flows are often abruptly dissected by a multitude of deeply incised streams, such as the Río Peje gorge.

The 2600-m site has considerable deposits of granular andesitic ash, and some soils near the 2000-m site appear to be weathered from old ash deposits. Farther north, the soils appear to be derived from basalt, such as in the southern half of La Selva. One of the most striking changes with increasing elevation is the notable increase in organic matter in and on the soil. Above about 1400 m, there is considerable humus accumulation on the soil surface, which is usually soft and mucky wherever drainage is poor.

At La Selva (Fig. 2), annual rainfall averages 4015±716 mm (n=26) and mean annual temperature is 24.1° C. Hartshorn (in Pringle et al. 1984) interpreted the abundance of *Carapa guianensis* (Meliaceae) on well-drained slopes at 300-500 m in the ZP as an indication of higher rainfall than at La Selva, where *C. guianensis* is the second most important tree species in swamp forest (Hartshorn 1983). Rainfall data from stations within 15 km of the transect (Table 1) indicate the typical orographic increase in annual rainfall. The natural vegetation suggests that average annual rainfall could be as high as 6000 mm in the 1500-1800-m section of the transect.

METHODS

The 1985 Operation Raleigh (OR) expedition established a trail network and six study sites at elevations of approximately 100, 500, 1000, 1500, 2000, and 2600 m (Fig. 1). At each study site a 100x100-m (1.0 ha) permanent plot was installed and inventoried by OR venturers. Inventory data (≥10 cm dbh) are being used to analyze tree species distribution, life form,



Location of study sites (⊙) along an altitudinal transect between the La Selva Biological Station and Volcan Barba, Costa Rica

Fig. 1. Map of the Braulio Carrillo complex and study sites between La Selva and Volcán Barva. In April 1986 the La Selva Protection Zone and the Forest Reserve area were added to Braulio Carrillo National Park. Adjustments (not shown) to the western boundary include the 2000-m site in the National Park.

Fig. 2. Hand-held, oblique, aerial photograph of La Selva facilities, including the footbridge over the Río Puerto Viejo. The original field station is on the left, and the new laboratory is the large building with tiered roof. (Photograph by G. Hartshorn, March 1984.)

importance, diversity, basal area, and density along the altitudinal transect (Hartshorn et al., in prep.). On the permanent plots, J. Proctor is also collecting data on litter fall, standing crop, and decomposition.

NASA contracted OTS and the Tropical Science Center (TSC) to participate in a research project using remote sensing techniques to study tropical forest dynamics. TSC's responsibilities were to do detailed life zone mapping and to identify and describe homogeneous vegetation types (Peralta 1985a) in the San José quadrangle (1:200,000). The detailed field mapping of life zones was done on the 1:50,000 topographic maps produced by Costa Rica's Instituto Geográfico Nacional. Updated rainfall averages from the Instituto Meteorológico Nacional were used in conjunction with elevation to determine

TABLE 1. AVERAGE ANNUAL RAINFALL FOR SELECTED SITES NEAR THE PEJE SECTOR OF BRAULIO CARRILLO NATIONAL PARK, COSTA RICA

Site	Rainfall (mm)	Period (yrs)	Elevation (m)	Distance from PNBC (km)
La Selva	4,015	26	42	3 N
Tirimbina	4,446	8	200	6 W
San Miguel	4,627	17	500	11 W
Cariblanco	5,096	5	970	10 W
Vara Blanca	3,426	21	1804	5 W
Sacramento	3,268	11	2260	2 W

on a preliminary basis the life zone of each weather station in the study area, which was then compared to the ecological map of Costa Rica (Tosi 1969). An intensive field survey along roads and trails was used to determine life zone boundaries, which were connected generally along a topographic contour on the 1:50,000 base maps. Life zones from the base maps also were transferred to the 1:200,000 map of the San José quadrangle.

For primary forest typing, NASA requested TSC to focus on the La Selva-Volcán Barva transect. NASA required each vegetation type to have homogeneous cover, structure and physical factors, as well as a minimum area of 200x200 m. Homogeneity was interpreted not only as minimal variation of the physiographic factors on a specific land-form unit, but also as a repetitive pattern in variation of such factors as elevation, slope, drainage, etc. Aerial photos were used to locate some homogeneous areas, but most were found by ground searches. The La Selva and OR permanent plots were used as parts of homogeneous areas. In each homogeneous area, information was taken on elevation, slope, exposure, canopy height, stand basal area, and principal canopy tree species. A prism (BAF=5) was used to estimate basal area for trees 10 cm or more in dbh.

In a second-phase subcontract, TSC conducted forest inventory and type mapping on two 1.0-km^2 plots near or including the OR 1000-m and 2000-m sites (Peralta 1985b). These large plots were located on recent aerial photos and the 1:50,000 topographic maps prior to field installation using easily recognized reference points. Each 1000x1000-m plot was subdivided into a 100x100-m grid. At each grid point the following data were taken: percent multiple slope; geomorphologic features; forest type; and total height, bole height, dbh, and species for all trees $\geq$10 cm dbh. Geomorphologic categories

include hill, hilltop depression, valley, and slope. Primary forests are classified into dense, open, and wind-shortened; the last may be dense, but of lower stature than normal forest in the area. The field data were used to prepare a 1:5,000 map of landforms and forest types in each 1.0-km^2 plot.

RESULTS AND DISCUSSION

Life Zones

Detailed mapping verifies the existence of four life zones and two transitions along the altitudinal transect between La Selva and Volcán Barva (Peralta 1985a). The La Selva Biological Station is entirely within the tropical wet forest life zone. The cool transition of this life zone begins at about 250 m elevation in the lower ZP, extending up to about 600 m. In the upper ZP, the warm, perhumid transition of tropical premontane rainforest life zone occurs in a narrow band between about 600 and 800 m. Non-transitional tropical premontane rainforest life zone occurs from about 800 to approximately 1450 m in the Peje sector of PNBC. Tropical lower montane rainforest life zone extends from about 1450 to 2500 m on the Barva massif. Tropical montane rainforest life zone occurs above 2500 m on Volcán Barva.

Our detailed life zone mapping differs only in minor ways from the small-scale (1:750,000) ecological map of Costa Rica (Tosi 1969). We believe that warm transition of tropical premontane wet forest life zone does not occur in the Río Frío-Puerto Viejo region, hence La Selva is entirely within the tropical wet forest life zone. Our field observations indicate that the changeovers from non-transitional to cool transition of tropical wet forest life zone and from the latter to warm, perhumid transition of tropical premontane rainforest life zone occur at lower elevations than suggested by the ecological map of Costa Rica. The narrowness of the latter transition may have precluded illustration on such a small-scale map.

Two major ecological changes along the altitudinal transect are apparent. The changeover from non-transitional tropical wet forest life zone to the cool transition of the same life zone coincides with the abrupt loss of dominance and decline in abundance of *Pentaclethra macroloba* (Mimosaceae). The second obvious change is between tropical premontane rainforest and tropical lower montane rainforest life zones. The latter is characterized by brownish, epiphytic mosses covering virtually everything and by the abundant, scandent bamboo, *Chusquea pohlii* (Graminae) in the forest understory. In the Peje sector, we happened to hike independently and in opposite directions across this changeover in life zones. Each of us experienced a distinct impression of entering a forest typical of much lower or higher elevations, respectively. Other life zone changes along the altitudinal transect are much more subtle and far less obvious.

We were surprised by the altitudinal breadth of the changeover between life zones. Except for the above-mentioned sharp decline of *P. macroloba*, life zone changes usually could be detected over an elevational range of about 100 m. Life zone boundaries generally are not sharply defined in the forest. Because maps require thin lines, we tried to determine life zone boundaries near the midpoint of these changeover areas. Based on life zone theory (Holdridge 1967; Holdridge et al. 1971), we expected a well-defined change between tropical premontane and lower montane rainforest life zones. Despite our initial impressions mentioned above, we concluded that the change between these two life zones occurs gradually between 1300 and 1600 m. The premontane and lower montane altitudinal belts are separated by the frost line, reflecting floristic rather than physiognomic differences. Thus the altitudinal breadth of the changeover between these two life zones is surprising. Much more floristic work needs to be done to determine how broad or narrow the change is between these two distinctive life zones in PNBC.

Together, tropical premontane and lower montane rainforest life zones comprise 75% of the Braulio Carrillo complex (Table 2). Very minor, disjunct areas of cool transition tropical wet forest life zone occur in the original PNBC. Non-transitional tropical wet forest life zone occurs only in the lower ZP (including La Selva). The disproportionately small amount of protected primary forests at low elevations could be a serious limitation to maintaining viable populations of species that migrate altitudinally in the Braulio Carrillo complex (Pringle et al. 1984).

Principal Types of Primary Forests

The following brief characterization of forest types is based on the descriptions of homogeneous areas (Peralta 1985a). By no means is this meant to be a comprehensive treatment of primary forest types along the La Selva-Volcán Barva transect. There are several probable causes for incompleteness: (1) focus on the Operation Raleigh study sites; (2) inaccessibility to much of the rugged middle and upper elevations; and (3) the authors' familiarity with the lowland forests in and near La Selva.

Six homogeneous study sites (8, 9, 9a, 11, 13, 22) were sampled in non-transitional tropical wet forest life zone, ranging in elevation from 33 to 100 m (Table 3). The principal forest type (Fig. 3) is characterized by the dominance of *Pentaclethra macroloba*, whose crowns form the base of the forest canopy (30-40 m in height). Other frequent canopy trees include *Apeiba membranacea* (Tiliaceae), *Brosimum lactescens* (Moraceae), *Goethalsia meiantha* (Tiliaceae), *Laetia procera* (Flacourtiaceae) and *Terminalia amazonia* (Combretaceae). The abundance of subcanopy palms in this forest type is impressive, particularly *Iriartea gigantea*, *Socratea durissima*, and *Welfia georgii*.

TABLE 2. DISTRIBUTION OF ECOLOGICAL LIFE ZONES IN THE BRAULIO CARRILLO COMPLEX, INCLUDING LA SELVA (see Figs. 1 and 2)

Tropical Forest Life Zone	Elevation (m)	Area (ha)
Tropical wet	35-250	2,604 [5.8%]
Tropical wet, cool transition	250-600	3,412 [7.6%]
Premontane rain, perhumid transition	600-800	4,355 [9.7%]
Premontane rain	800-1450	18,634 [41.5%]
Lower montane rain	1450-2500	15,132 [33.7%]
Montane rain	2500-2906	764 [1.7%]

The swamp forest of La Selva (site 9) is a distinctive forest type, even though it is also dominated by *P. macroloba*. Typical tree species in this swamp forest type include *Astrocaryum alatum* (Palmae), *Carapa guianensis* (Meliaceae), *Otoba novogranatensis* (Myristicaceae), *Pithecellobium valerioi* (Mimosaceae) and *Pterocarpus officinalis* (Fabaceae).

Three homogeneous study sites (23, 24, 25) were located in the cool transition of tropical wet forest life zone. Characteristic tree species include *Billia colombiana* (Hippocastanaceae), *Calophyllum brasiliense* (Guttiferae), *Micropholis crotonoides* (Sapotaceae), *Euterpe macrospadix* (Palmae) and *Vochysia ferruginea* (Vochysiaceae). Despite elegant *Euterpe* palms on the ridges and beautifully variegated *Geonoma epetiolata* in the forest understory, the abundance of subcanopy and understory palms is conspicuously less in this forest type than in the lower elevation forest types.

Only one homogeneous study site (27) was sampled in the narrow perhumid transition of tropical premontane rainforest life zone (Fig. 4). In addition to previously mentioned *Calophyllum, Micropholis,* and *Vochysia*, other characteristic tree species include *Alchornea latifolia* (Euphorbiaceae) and *Macrohasseltia macroterantha* (Flacourtiaceae).

Three homogeneous areas (2,26,36) were located in non-transitional tropical premontane rainforest life zone. Site 36, at 1260 m, has the highest stand basal area (36.9 m^2/ha) of the 21 study sites along the La Selva-Volcán Barva transect. Characteristic tree species in this forest type include *Aiouea costaricensis* (Lauraceae). *Guarea pittieri* (Meliaceae), *Hieronyma guatemalensis* (Euphorbiaceae), *Meliosma vernicosa* (Sabiaceae) and *Ocotea ira* (Lauraceae). Except for *Prestoea longipetiolata*, subcanopy and understory palms continue to decline in abundance at these elevations. Compared to lowland forest types, there is a marked increase in tree ferns (*Cyathea, Cnemidaria, Dicksonia, Nephelea, Trichipteris*) in this premontane rainforest type.

Six homogeneous areas (28, 29, 31, 33, 34, 35) were sampled in tropical

TABLE 3. CHARACTERISTICS OF HOMOGENEOUS STANDS OF PRIMARY FOREST SAMPLED ALONG THE LA SELVA-VOLCAN BARVA TRANSECT

Site No.	Elevation (m)	Canopy Height (m)	Basal Area (sq. m/ha)
Tropical wet forest life zone			
9	33	40	28.3
8	40	35-40	24.3
11	40	35-40	28.3
9a	45	35	26.4
13	70	30-40	24.3
22	100	35-40	–
Tropical wet forest, cool transition life zone			
24	420	30-35	–
23	500	35-40	25.0
25	520	25-30	27.5
Tropical premontane rainforest, perhumid transition life zone			
27	750	35	27.0
Tropical premontane rainforest life zone			
2	800	30-35	–
26	1000	30-35	32.5
36	1260	20-30	36.9
Tropical lower montane rainforest life zone			
34	1500	25-30	33.6
35	1520	14-17	9.8
33	1635	25-30	–
31	1755	20-25	29.3
28	2000	20	26.7
29	2130	20-25	20.8
Tropical montane rainforest life zone			
37	2650	20-23	25.0
38	2680	20-23	–

Fig. 3. Tropical wet forest canopy dominated by *Pentaclethra macroloba* (with compact, round crown). The few, tall subcanopy palms visible are *Iriartea gigantea*. Liana-covered crowns are noticeable in the lower left. Several canopy gaps appear as dark areas. (Hand-held, oblique, aerial photograph of La Selva by G. Hartshorn, October 1973.)

lower montane rainforest life zone (Fig. 5). Typical tree species include *Billia hippocastanum* (Hippocastanaceae), *Guatteria oliviformis* (Annonaceae), *Hieronyma poasana* (Euphorbiaceae), *Quercus tonduzii* (Fagaceae) and *Turpinia occidentalis* (Staphyleaceae). Especially abundant in this forest type are the understory palm, *Geonoma hoffmaniana*, and the scandent bamboo, *Chusquea pohlii*.

Two homogeneous areas (37, 38) were located in tropical montane rainforest life zone. Characteristic tree species include *Brunellia costaricensis* (Brunelliaceae), *Didymopanax pittieri* (Araliaceae), *Drimys winteri* (Winteraceae), *Ilex vulcanicola* (Aquifoliaceae) and *Weinmannia pinnata* (Cunoniaceae).

Few tree species are restricted to one forest type or even to one life zone (Holdridge et al. 1971). Our initial results clearly conform with the general pattern of tree species occurring in more than one forest type. Even some of the tree species listed above to characterize particular forest types have appreciably broader altitudinal distributions. For example, *Carapa guianensis*, *Iriartea gigantea* and *Terminalia amazonia*, which are characteristic tree species

Fig. 4. Primary forest trees left during conversion to pasture in tropical premontane rainforest. The flat-crowned trees are *Vochysia ferruginea*, approximately 40 m tall. (Photograph by G. Hartshorn, January 1985.)

in tropical wet forest types, also occur occasionally to frequently in the cool transition forest type. The reverse pattern occurs with *Calophyllum brasiliense* and *Vochysia ferruginea*, which are less frequent in La Selva forest types than in the cool transition. At higher elevations such tree species as *Billia hippocastanum*, *Didymopanax pittieri*, *Drimys winteri* and *Weinmannia pinnata* have broad altitudinal distributions in lower montane and montane forest types.

Several valuable timber species have more robust populations in the lower Peje Sector of PNBC than at the La Selva Biological Station. *Aspidosperma cruentum* (Apocynaceae), *Calophyllum brasiliense* (Guttiferae), *Dalbergia tucurensis* (Fabaceae), *Hieronyma oblonga* (Euphorbiaceae), *Lecythis ampla* (Lecythidaceae) and *Minquartia guianensis* (Olacaceae) rare to occasional tree species in La Selva (Hartshorn and Poveda 1983)—are much more abundant in the cool transition forest type.

The frost or critical temperature line (Holdridge 1967) that separates tropical premontane and lower montane altitudinal belts is the most important floristic division on the La Selva-Volcán Barva transect. A few lowland tree species, e.g. *Dendropanax arboreus* (Araliaceae), *Geonoma interrupta* (Palmae), *Dussia macroprophyllata* and *Pterocarpus hayesii* (both Fabaceae),

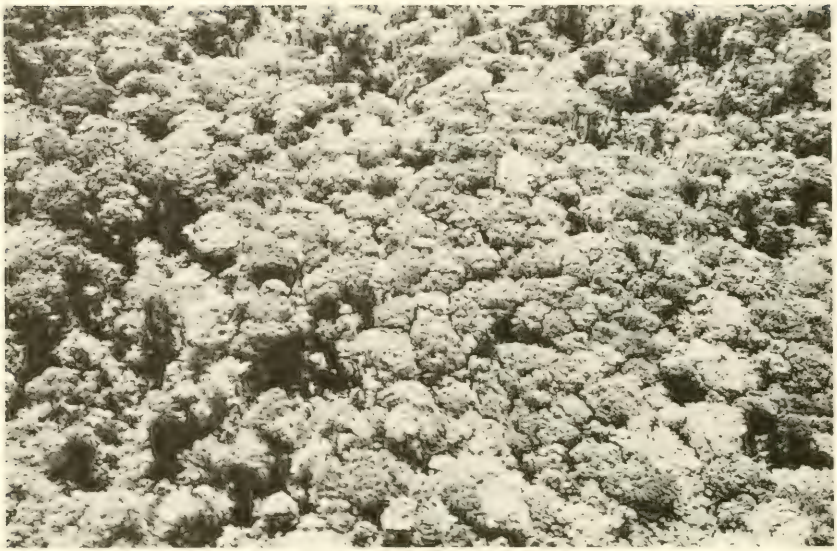


Fig. 5. Tropical lower montane rainforest canopy in Braulio Carrillo National Park. The smooth canopy (center) is a successional patch dominated by two tree species and surrounded by primary forest with a more heterogeneous canopy. (Hand-held, oblique, aerial photography by G. Hartshorn, March 1979.)

extend to the upper limit of tropical premontane rainforest life zone. Similarly, high-elevation tree species, such as *Viburnum mexicanum* (Caprifoliaceae) and the previously mentioned *Didymopanax*, *Drimys* and *Weinmannia*, extend down to the lower limit of tropical lower montane rainforest life zone. The frost line boundary between closely related congeners is particularly striking in such tree genera as *Billia*, *Brunellia*, *Clethra* (Clethraceae), *Dendropanax*, *Guatteria*, *Guettarda* (Rubiaceae), *Hieronyma*, *Ilex*, *Tetrorchidium* (Euphorbiaceae) and *Vismia* (Guttiferae).

There are at least two conspicuous exceptions to the frost line as a species boundary: *Alchornea latifolia* is a frequent canopy tree from 300 to about 2300 m; *Symphonia globulifera* (Guttiferae) is a common canopy tree between 1200 and 1800 m, yet at La Selva it is an occasional treelet. This is not an ecocline, because *S. globulifera* is a large canopy tree in the lowland swamps of Tortuguero and Corcovado National Parks.

Several north temperate tree genera occur in tropical lower montane and montane rainforest life zones. *Alnus*, *Cornus*, *Magnolia*, *Prunus*, *Quercus*, *Symplocos* and *Viburnum* are conspicuous components in these high-elevation

forest types. Also present above the frost line is the southern hemisphere conifer *Podocarpus.*

Large-Scale Patterns

We began the second phase of the NASA field work intending to map forest types according to Holdridge's association concept. As part of the hierarchical life zone classification system, Holdridge (1967:33-34) defines an association "as a range of environmental conditions within a life zone together with its living organisms of which the total complex of physiognomy of plants and activities of the animals are unique." Holdridge also affirms that associations can be mapped.

Surprisingly, no detailed mapping of associations has been done using Holdridge's life zone system. The oft-cited association map of the Chiang Mai area of Thailand (Holdridge et al. 1971) is at a varying scale of 1:25,000 to 1:15,000. This is not comparable to our attempt to map associations on 1.0 km^2 at a scale of 1:5,000.

The presence of certain tree species on specific landforms and their absence on different landforms is readily apparent. For example, on the grid at 1000 m elevation, *Calophyllum brasiliense, Euterpe macrospadix* and *Vochysia ferruginea* consistently dominate hills and ridges, whereas *Alchornea latifolia, Hieronyma guatemalensis* and *Pterocarpus hayesii* usually occur near the creeks. An initial impression is that these differences indicate two distinct forest associations; however, intensive field reconnaissance to locate the boundary between these two associations reveals a gradual transition from creek edge to hilltop. This conforms with the altitudinal variation in tree species distributions on the La Selva permanent plots (Lieberman et al. 1985). The extremely complicated spatial distribution of landforms, coupled with elevational differences, further obscures any tendency to form distinctive natural associations. More detailed, large-scale mapping of floristic and physiognomic patterns will be needed to test the validity of natural associations in tropical forests.

The 1.0-km^2 plot near 1000 m is a mosaic of dense primary forest and open primary forest. The latter is often associated with stream courses due to poor drainage of the narrow floodplain. However, landslides are common on the steep slopes, occasionally resulting in large openings in primary forest. Dense primary forest dominates the 1.0-km^2 plot near 2000 m. Four other natural forest types occur patchily in the plot: open primary forest on flat topography with poor drainage; wind-shortened primary forest in an area exposed to strong northeasterly winds; dense primary forest on very steep slopes; and open primary forest on very steep slopes. The difference between the two types on very steep slopes probably is associated with differences

in soil stability. The remaining vegetation types on the plot are successional patches following pasture abandonment.

In both 1.0-km^2 plots, forest types are strongly influenced by physiographic position. Tall, dense primary forest generally occurs on sloping landforms, probably due to adequate drainage. On hilltop depressions and flat floodplains, the primary forest may be not only more open, but also shorter (e.g. site 35). Large-scale patterns in the distribution of forest types are further obscured by the dynamic nature of tropical forests (cf. Hartshorn 1980). A June 1986 windstorm destroyed 150-200 ha of primary forests between 1100 and 1300 m in the Peje sector of PNBC. Landslides (cf. Garwood et al. 1979) also are a major cause of canopy openings.

The 2000-m grid has a much greater quantity of fallen trees than the 1000-m grid. This may be partially explained by slower decomposition and greater abundance of trees with resistant wood, e.g. *Quercus tonduzii*, at higher elevations. The upper grid also has a much denser understory than the lower grid. On both grids we noticed several cases of tiny streams flowing under the base of a mature canopy tree. The formation of a new streamlet during the lifetime of a canopy tree suggests that geological processes may be quite rapid on wet tropical mountains.

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BRAULIO CARRILLO AND THE FUTURE: ITS IMPORTANCE FOR THE WORLD

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In thinking about the marvelous accomplishment represented by the newest addition to Braulio Carrillo National Park in Costa Rica, it is necessary first to think about the world context in which this event has occurred. First and foremost, the world is a very different place from what it was 50 years ago. Some of the major problems that help to make it so are problems in population, problems of poverty, and problems of our ignorance of tropical resources. In the face of these problems, we are starting to realize that we really are all citizens of a single world, and that we are affecting that world with a strength and a pressure that was unimaginable even a few decades ago. This pressure creates conditions that are unprecedented in the history of the world; we must respond to these conditions because they will shape the quality of that world and the kind of life that our children and grandchildren and the children and grandchildren of people all over the world will find in the future.

I will now recapitulate some of the themes that you have heard discussed during the course of this symposium. The first of these, and one of the most important, has to do with the sheer beauty and interest and diversity of tropical forests. The grandeur of the interactions that take place in such forests has no parallel anywhere else on earth. As other speakers have made abundantly clear, we are just barely beginning to learn how to recognize and understand these interactions, and doing so much more slowly than we collectively are destroying the forests in which they take place.

Another theme is the theme of the poor—the relentless pressure that poverty imposes on the forests. Poverty enforces a lack of options for about a fifth of our fellow human beings, and brings many of them to the necessity of using the forests. The destruction of tropical forests by people living in absolute poverty is our problem just as much as it is theirs. We are all part of a single human race, numbering some five billion people; and if, by our economic systems, we consign so many to a life of relentless poverty, we should

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not be surprised, although we are properly concerned, when these same people destroy the productive capacity of natural resources.

The many products that can come from tropical forests were stressed in several different papers in this symposium. These products represent opportunities; they are the common property of all humankind. If we allow them to disappear permanently from the face of the earth without caring, they will be denied to everyone, rich or poor, forever.

The sheer interest and complexity of the interactions in tropical forests are so great that we can barely understand them. Undisturbed, tropical moist forests are one of the most productive ecosystems on earth; when they have been cut over, they are often replaced by landscapes that are of no benefit to anyone. Presumably we could learn to manage the forest for long-term and sustainable productivity of products of interest to us. Instead, we seem to be content, as expressed by our passivity, to allow it to be consumed or to consume it; to allow ourselves to be part of a process which does consume it as surely as we are consuming fossil fuels, irrevocably and completely. Slash and burn agriculture, or shifting cultivation, which when practiced at low population density allows the forest to recover and be used again, is highly destructive when practiced at higher population densities because the soils of the tropics, which are often poor in nutrients, are shallow. Under these circumstances, shifting cultivation poses a genuine problem to the construction of sustainable agricultural systems and to the support of human life in these areas. The knowledge that we have is rarely utilized fully by shifting cultivators, who also characteristically have no access to credit that would allow them to improve their local conditions.

Viewing these problems more formally, the world population has doubled from its level of about 2.5 billion in 1950—just 36 years ago. Over this period, during which the United States has enjoyed the greatest prosperity by the greatest number of people ever known in the history of the world, with the greatest opportunities available to them, the world population has doubled. The population of the developed world—Europe, the Soviet Union, Japan, North America, Australia, and New Zealand—has grown markedly, the population of China has nearly doubled, but the population of the less developed world, which consists almost exclusively of countries that lie wholly or partially in the tropics or subtropics, has, during that same period of time, gone from 1.1 billion to 2.7 billion people—it has gone up two and a half times. Small wonder that we see the gold miners going into Corcovado National Park—the conditions of living that determine human actions in the tropics have changed remarkably. Situations of this sort can be understood only in the whole social and economic context of which we and they, and all the people in Costa Rica and all the people in the United States, are a part. Only when this point becomes clear can we hope to find ways to make the

overall situation better. If we fail to find ways to provide alternative opportunities for the gold miners in Corcovado and the squatters in parks and reserves throughout the world, we can forget the possibility of saving some of these parks—they will all be consumed, and in less than a few decades.

Most demographers believe that the world population will stabilize somewhere in the second half of the 21st century at between 10 and 12 billion people. Tropical forests, however, are being destroyed by the *present* population at a rate that would lead to their total loss within about 80 years; and that rate of destruction will accelerate greatly as the population increases. By the year 2020, some five billion people, equal to the entire world population now, will be living in tropical or subtropical countries. The increased pressures that such a population will bring to bear on all natural resources, including forests in the tropics and subtropics, is a topic on which we rarely dwell.

During the 70-year period, 1950-2020, the proportion of people living in the developed world will drop from about one out of three people in the world to one out of six. In contrast, the proportion of people living in the largely tropical and subtropical countries of the developing world will increase from about 45% of the world population to nearly two-thirds. The people who live in the developed world control about 80 to 90% of all the commodities that maintain their standard of living at its present level, a fact that would cause extensive stress even if populations were stable, but which must do so as they change drastically in proportion.

An additional factor of the greatest importance, to which I have already referred, is the extensive poverty that exists within the countries themselves. More than one out of three of the estimated 2.7 billion people who live in countries that are partly or wholly tropical or subtropical live in what the World Bank defines as absolute poverty. Absolute poverty is a condition of living in which a person cannot be sure that he will find food, shelter, or clothing for himself or his family from one day to the next. Half of the estimated one billion people who are living in absolute poverty are actively malnourished. In addition, UNICEF has estimated that more than 10 million babies under the age of four starve to death in the world every year. It is uncertain how many additional people starve to death each year, but 10 to 20 million would not be an unreasonable estimate. Considering, therefore, that some 75,000 to 100,000 people starve to death each day, it is all but unimaginable that certain commentators would maintain that there is no crisis in the world at the present time. Starvation, of course, is but one end of the spectrum of malnutrition, which reduces tens of millions of people to a condition of incomplete physical and mental development with each passing year, owing to their lack of adequate supplies of food, and by doing so, consigns them to unproductive lives.

The final factor I wish to discuss in this section concerns our ignorance of how to convert most tropical lands into sustainable agricultural and forestry systems that would have the capability of supporting human lives at a level of dignity we might consider reasonable. There is, in fact, a great deal of knowledge available about how to cultivate such lands, and concerning the ways in which better soils in the tropics might be produced to provide even better yields, and even concerning the ways in which tropical and subtropical forests might be made to produce increased quantities of commercially valuable products without being destroyed completely. All of these options, however, depend upon understanding the forests better and applying that knowledge actively, constructively, and well to the creation of such sustainable systems. In addition, the needs of the people living in absolute poverty, who have no options but to destroy their own natural resources at the present time, must be taken seriously and ways must be sought to provide for them at a reasonable level.

Taken together, these factors underlie and cause a very rapid rate of destruction of tropical and subtropical forests everywhere in the world. In 1980, the Food and Agriculture Organization of the United Nations (FAO) suggested that 44% of the tropical closed forests had already been clear-cut by that time with 1.1% of the remainder being destroyed. As we have already discussed, the explosive growth of human populations in the tropics, the widespread deterioration of these forests as a result of widespread shifting cultivation, and the unequal distribution of this destruction mean that, for many tropical areas, all of the forests will be gone within a few decades. At the present time, however, about one-eighth of all tropical closed forests are being clear-cut each decade; thus, we have lost approximately this amount of forests since 1975.

In the next 10 years, even if there were no additional growth in population, even disregarding shifting cultivation and also disregarding the uneven distribution of forest growth, another eighth of the remaining tropical closed forests will be clear-cut. In little more than 75 years, all of the tropical forests would have been clear-cut, even using these unrealistic assumptions. Against this background, it is notable that the present democratically elected Brazilian government is the first in that country to put the problem of the poor on the national agenda, and to acknowledge that poverty is a serious problem for the future development of Brazil. By doing so, they have recognized that population growth in itself is not the major factor destroying natural resources in tropical countries, but that the neglect of widespread poverty is even more important and much less emphasized in most discussions of the problem.

The problems of conservation in the tropics can be addressed effectively only by regarding them as a part of the overall problem of sustainable land

use in these regions. If human populations can be stabilized in number, if the problems of widespread poverty in tropical and subtropical countries can be addressed effectively, and if the knowledge we have about how to cultivate these lands on a sustainable basis can be made widely available and implemented, then the conservation of natural areas and the preservation of species will come about as a part of the overall system. If we do not address all of these problems, then the tropical forests, along with the very poorly known species of plants, animals and microorganisms in them, will be lost before we have even a rudimentary idea of their beauty, interest, scientifically important characteristics, and potential uses for human welfare.

Where do all of these consequences lead for the United States? As newspapers, magazines and television broadcasts make clear, they lead to political instability, and to a situation in which governments tend to last only for relatively short periods of time. This comes about largely because the governments, and those of us who work together with them, neglect the very large numbers of poor people—people who will always have the capacity, the will, and the lack of alternative purpose that make it desirable from their point of view to overthrow the present government. The neglect of these problems leads to a situation in which the creation of a stable global ecosystem is virtually impossible. It leads to a situation in which population growth in the United States and other developed countries will continue to be dominated by immigration simply because, for many people in the world, there are no other options that are as attractive. As the human population increases, the global ecosystem no longer has the buffering capacity that it once had; and as Jon Tinker has aptly pointed out, catastrophes become much more apt to happen. We are all part of one global ecosystem, whether we choose to emphasize this fact or not, and the future that we share depends directly upon this point. When we provide foreign assistance to other countries in the world, we should realize explicitly that we are not doing so as a matter of charity, but rather that we are acting as responsible members of a human race who have great opportunities to improve the world situation and thus help ourselves and all human kind.

The most important aspect of the rapid destruction of tropical forests has to do with extinction. Extinction is important to us, even leaving aside the scientific and aesthetic problems associated with it, because human society is based directly on the properties of plants, animals and microorganisms. Only the capability of some 300,000 species of plants, algae, and some bacteria makes possible the biological productivity of the global ecosystem and all other organisms on earth, including anywhere from 4 million to 30 million species of animals, fungi and heterotrophic protists and bacteria, which depend on the activities of these organisms.

Viewed in this light, when we calculate that only 20 kinds of plants

provide some 85% of all of our food, directly or indirectly, and that three species alone—corn, rice, and wheat—provide about two-thirds of our food, then we must begin to wonder about the remaining 250,000 species of plants and what they might provide for us. This becomes all the more obvious when we realize that all of the 20 major crop plants were selected for cultivation between 2,000 and 10,000 years ago because they were crops that could easily be brought into cultivation by our Stone Age ancestors. Among the roughly 160,000 species of plants that occur in the tropics and subtropics, half of them in Latin America alone, there must be many on which an improved condition of human existence could be based.

Ample evidence from throughout the tropics makes it clear that extinction is proceeding rapidly in many areas. For example, in Hawaii, as shown by fossil and modern evidence, of the minimum number of 88 species of land birds that were present when the Polynesians landed some 1,500 years ago, only a tenth (nine species) still exists in viable populations, with an additional 19 species hanging on to existence in the fragments of forests that have been left behind in these islands. This history readily documents the process of extinction on a well-known island group and one which has, for the better part of a century, been managed by the wealthiest nation on earth.

Western Ecuador provides an additional example of an area where extinction is proceeding rapidly. Less than 10% of the area that was forested in 1950 still remains forested and, as the principles of island biogeography will indicate, a tenfold increase in area is generally associated with a doubling in the number of species. When a particular area is reduced to less than 10% of its original size, therefore, one can logically assume that half the species that were originally there are in danger of extinction. Perhaps a third of the plant species of western Ecuador were once endemic to that region, a number of plants that could have amounted to about 2,000 or 2,500 species, and we may, therefore, assume that at least 1,000 to 1,250 species of plants are already extinct or in danger of extinction in that one small region alone. Among these is a forest tree of the laurel family (Lauraceae), *Caryodaphnopsis theobromifolia*. This particular species, which is one of the very few members of the laurel family that has opposite leaves, used to be the most important source of building timbers in western Ecuador, both for houses and for furniture, but by the 1980s, fewer than 20 individuals were known to exist. It stands to reason that among the species that have already become extinct or are in danger of extinction in this area there were some that could have been used for building materials which were never utilized, and other that could have been valuable sources of drugs, and others that were simply beautiful or interesting. Among the latter, we might count *Epidendrum ilense*, one individual of which was found by Cal Dodson on a felled tree in a pasture in western Ecuador, but which has never been seen again in the wild.

Although this attractive orchid is genetically self-incompatible, it has been propagated vegetatively and is now widespread, both in botanical gardens and in the commercial trade. Over the last 20 years, however, the plant has never been seen again in the wild, and it is reasonable to assume that it is extinct. Finally, on Centinella Ridge behind Río Palenque, there are at least 100 plants known to occur which are still undescribed but which have never been found anywhere else. Since Centinella Ridge has been clear-cut over the past few years, we may assume that they, too, have largely been lost and that the majority of them did not occur anywhere else.

Similar calculations could be offered for the Atlantic forests of Brazil, although their clearing and destruction took place earlier than that of the forests of western Ecuador; only less than two percent of the original forested area still remains in a reasonably natural condition.

Madagascar, an island about twice the size of Arizona that lies about 250 miles off the east coast of Africa, presents a particularly important example of biological extinction. I would estimate that there were originally some 200,000 species of plants, animals, and microorganisms in Madagascar, of which probably 150,000 occurred nowhere else. Among them were all 21 living species of lemurs, one of the most interesting primitive groups of the order of the primates, the order of mammals to which we ourselves belong. The original vegetation of Madagascar has been largely destroyed with something like 5 to 10% still remaining in a relatively unaltered condition. Under the circumstances, we may assume that at least 75,000 species of plants, animals and microorganisms have already become extinct during the past century, or are in danger of extinction now, clinging to existence in small forested areas, in parks and reserves, and usually represented by very few individuals. What an enormous loss these species represent for us in terms of knowledge that supports us.

Summarizing up to this point, we may say that we are living in a time of maximum destructiveness of natural resources—a time when an explosively growing world population, widespread poverty that we mainly fail to recognize in our collective activities, and a lack of knowledge about how to produce sustainable agricultural and forestry systems in the tropics and subtropics, are leading to the extinction of a very large number of plants, animals and microorganisms—perhaps 20% of the total—during our lives. Considering that the world population is expected to stabilize somewhere in the second half of the next century, we can view the period in which we are living now as one of extreme catastrophe and one in which the decisions that are made will have the potential of leading to the preservation of plants, animals, and microorganisms that might otherwise be lost permanently. It follows that we have the greatest opportunities for study, for the increase of knowledge, and for the application of knowledge that will ever occur in the entire history of the

human race. More organisms are in existence now, more undisturbed natural ecosystems are in existence now and much more can be gained more easily now than will be the case at any point in the future. Regardless of how effective we may be in our efforts, we can be reasonably certain that approximately an eighth of the tropical forests that remain now will have been clear-cut over the next 10 years and that, over most of the tropics, nearly all of the forests will have been badly damaged or removed during our lives. Exceptions may be the western Brazilian Amazon, the interior of the Guianas in South America, and the central Zaire (Congo) Basin in Africa.

During the next 30 or 40 years, there will certainly be an unprecedented extinction of organisms. To those who might hold that extinction is normal and that what is going on now is simply routine, it should be pointed out that to find a comparable rate of extinction one needs to go back all the way to the end of the Cretaceous Period, some 65 million years ago, to find a comparable loss. The end of the Cretaceous was a time when perhaps more than half of all the species of organisms on land became extinct, changing the character of life on earth forever, placing the mammals, birds, and insects in the ascendancy, producing what we know as the modern world. The kinds of rates of extinction that are going on now during our lives are entirely comparable in scope, and need to be taken extremely seriously.

In confronting this problem, the best institutions that have been organized in developed countries such as the World Wildlife Fund and the Nature Conservancy, museums such as the California Academy of Sciences, botanical gardens and all other similar institutions that exist, must be utilized effectively and will make a substantial difference. Equally valuable and greatly to be cherished are organizations such as the Fundación de Parques Nacionales and the Fundación Neotropica in Costa Rica, Natura in Ecuador, and similar organizations that have grown up in tropical countries, which are dedicated to the understanding and preservation of nature and biological diversity in their respective countries. By using the institutions that we are fortunate enough to enjoy in the developed world as counterparts of those that exist in the less developed countries of the tropics and subtropics, we can help to improve the situation that we all will confront with increasing intensity. If parks and reserves can be seen as part of our common heritage and something we all need to help maintain, not as some remote effort that has little or no bearing on our own future, then we may be able to hope that some of them will actually be preserved.

In Costa Rica, there exists an incredible opportunity for effective action. This opportunity has been brought about by the efforts of many hardworking and intelligent people, both Costa Ricans and foreigners, over the past several decades. Their activities have resulted in the creation of a system of national parks and reserves that is the envy of the entire world and that comprises

approximately a tenth of the total area of the country. Costa Rica has presented a remarkable combination of democracy, literacy, effective action, and genuine attention to the preservation of natural resources that is unfortunately rare in the rest of the world. Nonetheless, the relentless destruction of forests outside these parks and reserves is proceeding more rapidly in Costa Rica perhaps than in any other country in the world. As a result of these pressures, the parks and reserves in Costa Rica will eventually be placed in extreme stress, and this stress should be a matter of concern to us all. Indeed, given the remarkable combination of events that have led to the creation of such a system of parks and reserves in Costa Rica, and such a high level of understanding of the environment, one may legitimately ask, "If it can't work in Costa Rica, where can it work?"

In considering this question, one should realize that fully a tenth of the biological diversity of Latin America exists in Costa Rica, where there are perhaps 9,000 of the 90,000 estimated plant species and comparable representations of the other groups of organisms, for example. In terms of biological diversity alone, then, Costa Rica is an extremely important objective and represents an important opportunity, one that we could logically emphasize greatly in our collective plans. Again, one must ask, if we really cannot assist our Costa Rican colleagues and friends in accomplishing what they want to accomplish in Costa Rica, are we really addressing the problem effectively anywhere?

In connection with the themes that I have been developing in this paper, many people ask whether the world will really eventually be in as bad a condition as I have projected, or whether somehow matters will work out so that things are not nearly so bad. The logical answer to that question, from my point of view, is that the world is going to be as good a place as we make it. We, as a human race, must decide what we are willing to tolerate and, in the face of all of our divisions, all of our national boundaries, the differences between rich and poor, and all of the interactions that link and divide us, we collectively must decide what we want. The nature of our decision is what will make the conditions for our children and grandchildren better or worse.

On a world scale, Costa Rica and its system of national parks, including the remarkable one that we have been celebrating in this symposium—Braulio Carillo—is utterly precious. The preservation of this system of parks is not a problem for Costa Ricans alone; rather it is a problem for all of us. In fact, the establishment of a comprehensive system of national parks and reserves represents one of the great accomplishments of the human race over the last 30 years; and in the face of this accomplishment, it is a privilege for all of us to have the opportunity of participating in the establishment of conditions that will make possible the perpetuation of this system for the enjoyment, appreciation, and benefit of all of those who come later. The magnificent

leadership of the MacArthur Foundation in providing a $1 million challenge grant has been matched by other foundations and individuals and has, during 1985, been crowned with success. Overall this effort represents an outstanding one which, if nurtured and cared for throughout the years to come, will still be a model 100 years from now, 500 years from now, and 1,000 years from now.

In conclusion, I would like to emphasize again that the peculiar, unique and difficult combination of factors that are destroying sustainable productivity of natural resources in the tropics and causing the extinction of so many species of organisms during our lives need not overwhelm us. We certainly face a unique challenge, but it is one to which we can and will respond, thus establishing the basic conditions for improving the quality of life and the opportunities for all of those who come after us.

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